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Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan VII. Allocreadiidae: *Allocreadium*

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Abstract This paper reviews nine identified and four unidentified species of *Allocreadium* Looss, 1900 (Trematoda, Digenea, Allocreadioidea, Allocreadiidae) and *Allocreadium* sp. of Kataoka and Momma (1934), *incertae sedis*, parasitic in freshwater fishes of Japan. Each species is described and figured with a summarized life cycle where known. Morphological characters of adult and cercarial forms of the type species *Macrolecithus gotoi* Hasegawa and Ozaki, 1926 support the previous hypothesis that *Macrolecithus* Hasegawa and Ozaki, 1926 is a junior synonym of *Allocreadium*. A neotype is designated for *M. gotoi* (now *Allocreadium gotoi* (Hasegawa and Ozaki, 1926)). The type locality becomes Lake Kizaki in Oomachi City, Nagano Prefecture, Japan. Keys to the two genera (*Allocreadium* and *Crepidostomum* Braun, 1900) of the family Allocreadiidae in Japan and to the nine identified species of *Allocreadium* in Japan are presented.
Key words: Digeneans, Allocreadiidae, *Allocreadium*, *Macrolecithus*, freshwater fishes, Japan, review.

Introduction

This is the seventh paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). Many species of the family Allocreadiidae Looss, 1902 *sensu* Caira and Bogéa (2005) of the Allocreadioidea Looss, 1902 *sensu* Cribb (2005) have been found in Japanese freshwater fishes. They are classified into two genera, *Allocreadium* Looss, 1900 and *Crepidostomum* Braun, 1900 (see below). This contribution deals with species of *Allocreadium* and *Allocreadium* sp. of Kataoka and Momma (1934), *incertae sedis*. The next will deal with species of *Crepidostomum*. The Introduction, Materials, and Methods for the review were given in the first paper (Shimazu, 2013).

Abbreviations used in the figures. c, cercaria; cbp, cercarial body proper; cp, cirrus pouch; ct, cercarial tail; cvd, common vitelline duct; e, esophagus; ed, ejaculatory duct; egg, eggs in uterus; ep, excretory pore; es, eyespot; esp, eyespot pigment; ev, excretory vesicle; fc, flame cell; ga, genital atrium; gp, genital pore; gpr, genital primordium; i, intestine; Lc, Laurer's canal; m, metraterm; Mg, Mehlis' gland; mr, mother redia; o, ovary; od, oviduct; os, oral sucker; ot, ootype; p, pharynx; pc, prostatic cells; pp, pars prostatica; pr, prepharynx; s, stylet; sd, sperm duct; sr, seminal receptacle; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; vd, vitelline duct; vf, vitelline follicles; vs, ventral sucker.

Superfamily Allocreadioidea Looss, 1902
Family Allocreadiidae Looss, 1902

Key to genera of the family Allocreadiidae in Japan

1. Oral sucker without muscular papillae ..... *Allocreadium* Looss, 1900
2. Oral sucker with three pairs of muscular papillae..... *Crepidostomum* Braun, 1900

Genus ***Allocreadium*** Looss, 1900
Allocreadium aburahaya Shimazu, 2003

(Figs. 1–3)

Allocreadium aburahaya Shimazu, 2003a: 121–122, figs. 4–6.

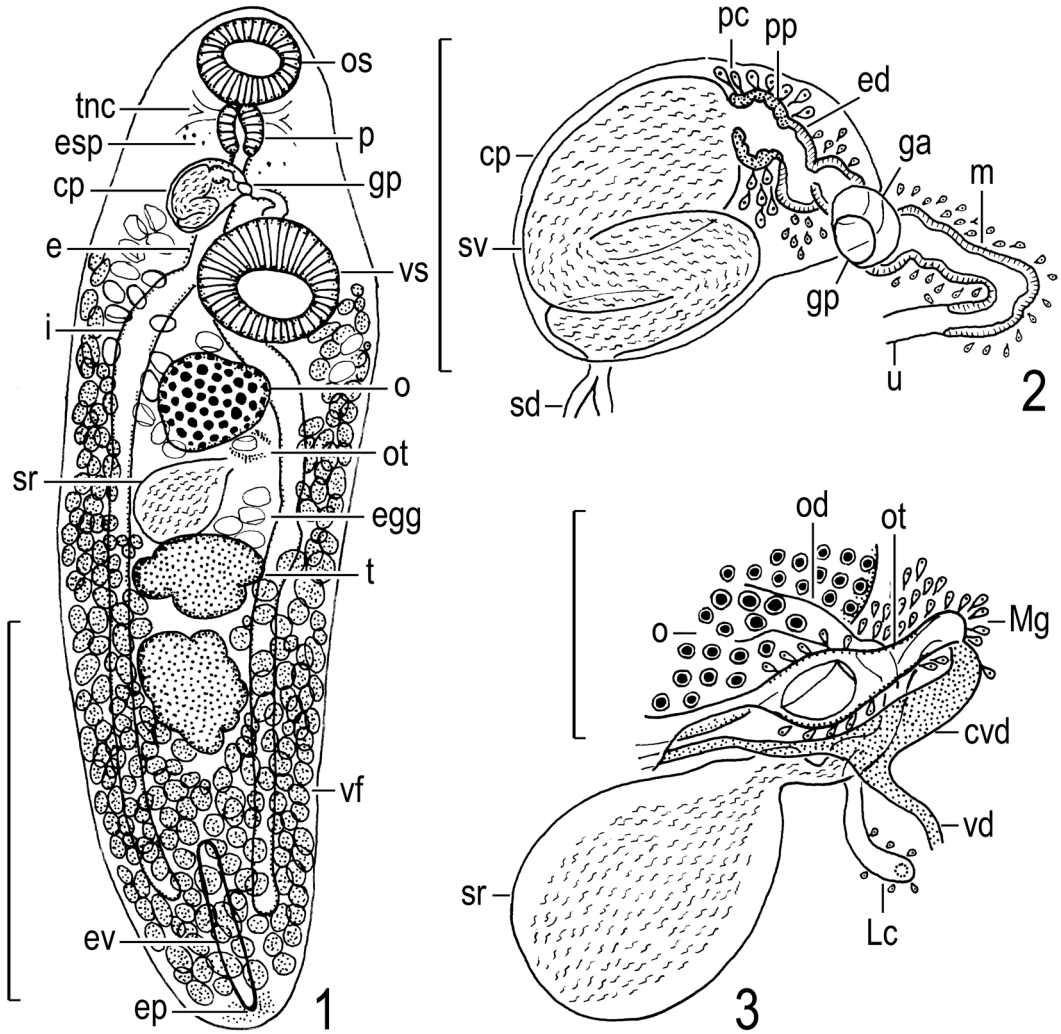
Host in Japan. *Phoxinus steindachneri* Sauvage, 1883 (Cyprinidae) (type host) (Shimazu, 2003a; this paper).

Site of infection. Intestine.

Geographical distribution. Nagano Prefecture: Hiroi River (type locality) at Kotobuki, Iiyama City (Shimazu, 2003a).

Material examined. 18 specimens (NSMT-Pl 5228, type series, holotype and 17 paratypes) of *Allocreadium aburahaya*, adult, whole-mounted, ex intestine of *Phoxinus steindachneri* (syn. *Phoxinus lagowskii steindachneri*), Hiroi River, 12 June 1999 (Shimazu, 2003a).

Description. After Shimazu (2003a), modified from the present study (Figs. 1–3). Body elongate, small, 2.56–2.90 by 0.66–0.80 (holotype 2.73 by 0.78); forebody 0.71–0.79 long, occupying 25–28% of body length. Tegument smooth.



Figs. 1–3. *Allocreadium aburahaya*, holotype (NSMT-Pl 5228), adult found in intestine of *Phoxinus steindachneri*. — 1, entire body, ventral view; 2, terminal genitalia, ventral view; 3, ovarian complex, ventral view. Scale bars: 1 mm in Fig. 1; 0.2 mm in Figs. 2–3.

Transverse nerve commissure dorsal to prepharynx or pharynx. Eyespot pigment present in forebody, scattered. Small gland cells present in forebody, with ducts opening at anterior tip of body (not illustrated). Oral sucker globular, 0.23–0.26 by 0.26–0.30, ventrally subterminal. Prepharynx present, very short. Pharynx elliptical, 0.12–0.14 by 0.11–0.12. Esophagus 0.24–0.35 long, surrounded by small gland cells, bifurcating dorsally to ventral sucker. Intestines (or ceca) ending blindly at some distance from posterior extremity of body. Ventral sucker globular, 0.29–0.33 by 0.32–0.39, located at about junction of anterior first and second fourths of body; sucker width ratio 1 : 1.2–1.4. Testes two, slightly indented irregularly, fairly large, 0.27–0.39 by 0.15–0.31, tandem, in middle third of hindbody, slightly separate. Sperm ducts two; common sperm duct absent. Cirrus pouch (or cirrus-sac) broad-ovate, 0.19–0.25 by 0.12–0.16, anterior to ventral sucker, including seminal vesicle, prostatic complex, and ejaculatory duct. Seminal vesicle tubular, S-shaped, large, in posterior two thirds of cirrus pouch. Pars prostatica globular, large, 0.02–0.03 by 0.04–0.05; prostatic cells numerous, small. Ejaculatory duct (or cirrus) short, undulating, 0.06–0.09 by 0.01–0.02, surrounded by small gland cells. Genital atrium small. Genital pore median, located at about midlevel of esophagus. Ovary single, globular or somewhat irregular, large, 0.26–0.31 by 0.21–0.27, median, between ventral sucker and anterior testis. Ovarian complex postovarian. Seminal receptacle canalicular, flask-shaped, large, 0.18–0.33 by 0.14–0.30, between ovary and anterior testis. Laurer's canal short, surrounded by small gland cells, running backward. Ootype vesicular, large, posterosinistral to ovary. Uterus coiled between anterior testis and cirrus pouch, between intestines, overlapping intestines anteriorly, sometimes extending posteriorly into intertesticular space; metraterm shorter than cirrus pouch, surrounded by small gland cells. Eggs fairly numerous, broad-ovate, operculate, light brown, 76–86 by 54–60 μm, unembryonated. Vitellaria follicular; follicles large, usually ventral or rarely dorsal to intestines, distributed in lateral fields of body from bifurcal level to near posterior extremity of body, separate anteriorly, confluent post-testicularly; vitelline ducts two; common vitelline duct serving as vitelline reservoir. Excretory vesicle I-shaped, thick-walled, dorsal to vitelline follicles, extending anteriorly to middle of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. This species and *Allocreadium shinanoense* Shimazu, 2003 (see below) were obtained from their respective hosts from the Hiroi River on 12 June 1999. The ootype (Shimazu, 2003a, fig. 6) should have been vesicular.

Life cycle. Not known.

Allocreadium brevivitellatum Shimazu, 1992

(Fig. 4)

Allocreadium sp.: Shimazu, 1988: 18, fig. 15.
Allocreadium brevivitellatum Shimazu, 1992: 213–215, figs. 1–3; Shimazu, 1994: 69, fig. 1.

Host in Japan. *Rhynchocypris percnurus* (Pallas, 1814) (Cyprinidae) (type host) (Shimazu, 1988, 1992; this paper).

Site of infection. Intestine.

Geographical distribution. Hokkaido: Sarurunto (or Saruruto-numa, a shallow pond in a marsh) at Toro, Shibecha Town (Shimazu, 1988, 1992; this paper).

Material examined. (1) 1 (NSMT-Pl 3055, *Allocreadium* sp. of Shimazu (1988), 1 paratype) of *A. brevivitellatum*, adult, whole-mounted, ex intestine of *Rhynchocypris percnurus* (syn. *Moroco percnurus sachalinensis* Berg, 1907), Sarurunto, 4 July 1984 (Shimazu, 1988, 1992). (2) 2 (NSMT-Pl 3678–3679, holotype and 1 paratype) of *A. brevivitellatum*, adult, whole-mounted, ex intestine of *R. percnurus*, Sarurunto, 3 September 1991 (Shimazu, 1992). One adult paratype and 1 immature voucher (NSMT-Pl 3680–3681) of Shimazu (1992) were not used. Probably, they had been lost on loan.

Description. After Shimazu (1992), modified from the present study (Fig. 4). Body elongate

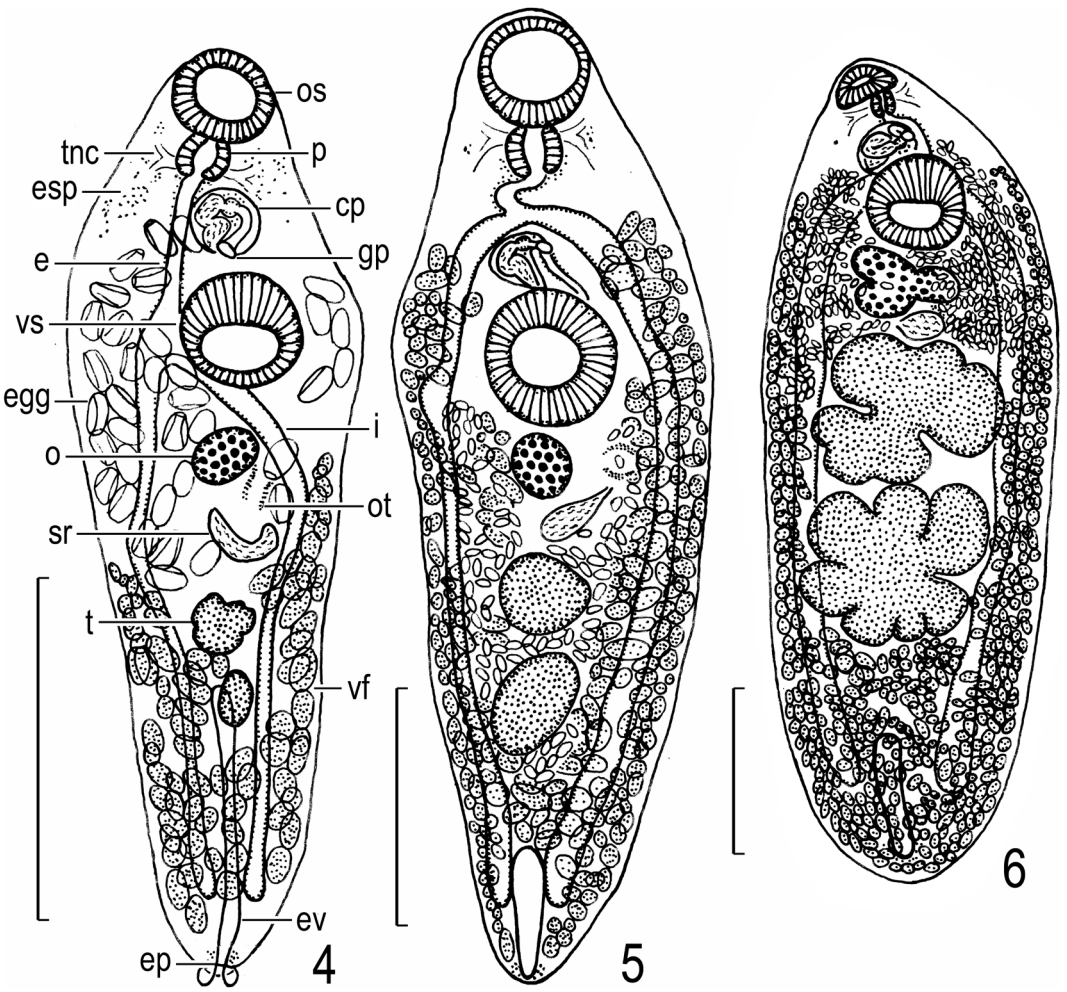


Fig. 4. *Allocreadium brevivitellatum*, holotype (NSMT-Pl 3678), adult found in intestine of *Rhynchocypris percnurus*, entire body, ventral view. Scale bar: 1 mm.

Fig. 5. *Allocreadium gotoi*, neotype (NSMT-Pl 2929), adult found in intestine of *Misgurnus anguillicaudatum*, entire body, ventral view. Scale bar: 1 mm.

Fig. 6. *Allocreadium hasu*, possible paratype (MPM Coll. No. 30006), adult found in intestine of *Opsariichthys uncirostris uncirostris*, entire body, ventral view. Scale bar: 1 mm.

ovate, small, 2.50–3.12 by 0.76–0.88 (holotype 2.68 by 0.84); forebody 0.70–0.96 long, occupying 27–31% of body length. Eyespot pigment dispersed. Oral sucker 0.24–0.26 by 0.29–0.33. Pharynx 0.12–0.14 by 0.10–0.16. Esophagus bifurcating dorsal to ventral sucker. Intestines extending to near posterior extremity of body. Ventral sucker 0.33–0.35 by 0.38–0.41; sucker width ratio 1 : 1.2–1.4. Testes smooth or indented irregularly, small, 0.16–0.26 by 0.13–0.20, almost tandem, separate or contiguous, in middle third of hindbody. Cirrus pouch spherical or elongate-oval, 0.20–0.30 by 0.13–0.21, anterior to ventral sucker. Seminal vesicle sinuous, in posterior third of cirrus pouch. Ejaculatory duct fairly long, slightly everted. Genital atrium small. Genital pore at about midlevel of esophagus. Ovary spherical to elliptical, small, 0.16–0.30 by 0.16–0.21, median. Seminal receptacle clavate, small, 0.18–0.28 by 0.06–0.07. Laurer's

canal as long as seminal receptacle or slightly shorter than it. Ootype postovarian. Uterus extending posteriorly to anterior testis in 3 specimens, but slightly beyond posterior testis in 1 specimen. Eggs 106–130 by 69–80 μm. Vitelline follicles distributed between ovarian level to near posterior extremity of body. Excretory vesicle reaching to middle of posterior testis; excretory pore posterodorsal.

Remarks. This species was found in Sarurunto, but not in Lake Toro nearby.

Life cycle. Not known.

Allocreadium gotoi (Hasegawa and Ozaki, 1926)

(Figs. 5, 7–10)

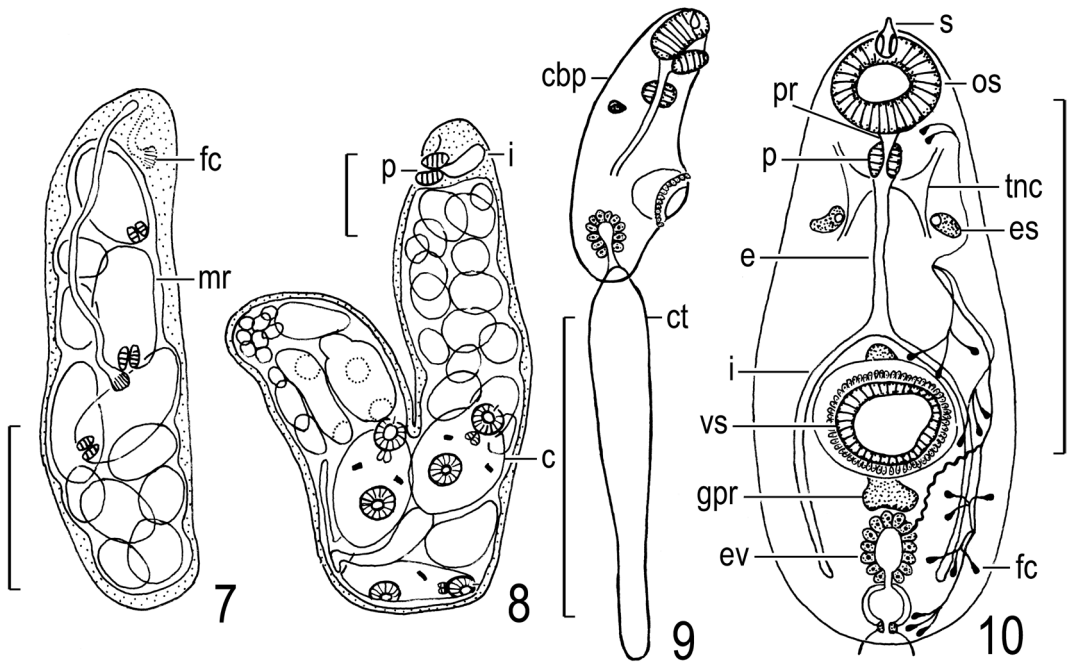
Macrolecithus gotoi Hasegawa and Ozaki, 1926: 225–227, fig. 1, 1 text table; Yamaguti, 1934: 333–334, fig. 38.

Allocreadium gotoi: Shimazu, 1988: 6–7, figs. 1–3; Shimazu, 1994: 69, fig. 2; Shimazu, 2002: fig. 7; Shimazu, Urabe, and Grygier, 2011: 29, figs. 34–35.

Hosts in Japan. *Misgurnus anguillicaudatus* (Cantor, 1842) (Cobitidae) (type host) (Hasegawa and Ozaki, 1926; Yamaguti, 1934; Shimazu, 1988, 1994, 2002; Shimazu *et al.*, 2011), *Gnathopogon elongatus elongatus* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 1988; Shimazu *et al.*, 2011), and *Gymnogobius opperiens* Stevenson, 2002 (Gobiidae) (Shimazu, 1988, 1994; this paper).

Site of infection. Intestine.

Geographical distribution. (1) Hokkaido: Oono River at Chiyoda, Hokuto City (Shimazu, 1988, 1994; this paper). (2) Miyagi Prefecture: Shichigo, Sendai City (Shimazu, 1988). (3) Nagano Prefecture: a small river at Midori, Iiyama City; a small river at Okada-machi, Matsumoto City; Furukawa River at Kamiimai, Nakano City; Komi (now Komi Town (?)); Lake Kizaki (type locality) in Oomachi City; and Lake Suwa at Suwa City (Shimazu, 1988, 2002; this paper). (4) Aichi Prefecture: Mikawa (central and eastern district of the prefecture) (Shimazu,



Figs. 7–10. *Allocreadium gotoi* (continued), life cycle, found in *Pisidium nikkoense*. — 7, sporocyst; 8, daughter redia; 9, cercaria, lateral view; 10, cercarial body proper, ventral view. Redrawn from Shimazu (2002). Scale bars: 200 μm.

1988). (5) Shiga Prefecture: Lake Biwa basin (Lake Biwa; Terasho, Koka City; and Zeze, Otsu City) (Shimazu, 1988; Shimazu *et al.*, 2011). (6) Kyoto Prefecture: Jonangu, Fushimi-ku, Kyoto City; and Miyakehachiman, Sakyo-ku, Kyoto City (Shimazu, 1988; this paper). (7) Hyogo Prefecture: Nishinomiya (Shimazu, 1988).

In China (Okino *et al.*, 2004).

Material examined. (1) 1 specimen (Ozaki's Collection, MPM Coll. No. 30009, labeled "DOJO," other data not given) of *Macrolecithus gotoi*, adult, serially sectioned, *Misgurnus anguillicaudatus* (Shimazu, 1988, 1995). Several sections of the anterior part of the forebody were missing. (2) Yamaguti's specimens of *M. gotoi*, ex intestine of *Mi. anguillicaudatus*: 2 (MPM Coll. No. 22570), adult, whole-mounted, Komi (Komi Village, now Komi Town, Nagano Prefecture (?)), 29 August 1927; 4 (MPM Coll. 22574), adult, whole-mounted, Jonangu, Fushimi-ku, Kyoto City, Kyoto Prefecture, 24 June 1940; 1 (MPM Coll. No. 22288, identified as *Allocreadium* by Shunya Kamegai on 19 April 1972), adult, whole-mounted, Miyakehachiman, Sakyo-ku, Kyoto City, 11 August 1941; 9 (MPM Coll. 22575, ex "stomach"), adult, whole-mounted, Mikawa (central and eastern district of Aichi Prefecture), 7 July 1937; 1 (MPM Coll. 22573, adult, whole-mounted), Nishinomiya (Nishinomiya City, Hyogo Prefecture), 11 June 1940; 7 (MPM Coll. No. 22567, ex "stomach and intestine"), adult, serially sectioned, whole-mounted, Shichigo, 3 August 1927; 1 (MPM Coll. No. 22571), adult, whole-mounted, Terasho, 8 July 1927; 1 (MPM Coll. No. 22568), serially sectioned, Zeze, 16 July 1928; and 4 (MPM Coll. No. 22294, locality not given), adult, whole-mounted, 23 June 1932 (Shimazu, 1988; Shimazu *et al.*, 2011). (3) 4 (NSMT-Pl 2931) of *A. gotoi*, immature, adult, whole-mounted, ex intestine of *Mi. anguillicaudatus*, Oono River at Chiyoda, Oono Town, now in Hokuto City, Hokkaido, 20 August 1983 (Shimazu, 1988). One immature and 2 adult specimens (NSMT-Pl 2932, Oono River, 23 August 1983) of Shimazu (1988) were not used. Probably, they had been lost on loan. (4) 5 (NSMT-Pl 2929) of *A. gotoi*, adult, whole-mounted, ex intestine of *Mi. anguillicaudatus*, Lake Kizaki, 28 August 1981 (Shimazu, 1988). Five adult specimens (NSMT-Pl 2929, Lake Kizaki, 24 July 1983) of Shimazu (1988) were not used. Probably, they had been lost on loan. (5) Shimazu's (2002) specimens of *A. gotoi*, ex intestine of *Mi. anguillicaudatus*, Nagano Prefecture: 39 (NSMT-Pl 5216–5219), immature, adult, serially sectioned, whole-mounted, a small river at Midori, 12 July 1987, 3 November 1989, 5 August 1990, 13 August 1999; 5 (NSMT-Pl 5222), immature, adult, a small river at Okada-machi, 3 August 1987; 6 (NSMT-Pl 5220), immature, adult, whole-mounted, Furukawa River in Toyoda Village, now Kamiimai, Nakano City, 17 June 2000; and 1 (NSMT-Pl 5221), immature, whole-mounted, Lake Suwa, 5 October 1991. (6) Yamaguti's specimens of *M. gotoi*, ex intestine of *Gnathopogon elongatus elongatus* [not *Gnathopogon elongatus caerulescens* of Shimazu (1988)], Lake Biwa: 1 (MPM Coll. No. 22572, labeled "*Macrolecithus gotoi* [Moroko]"), adult, whole-mounted, 9 July 1927; and 1 (MPM Coll. No. 22569, labeled "*Allocread*. [Moroko]"), adult, whole-mounted, 29 July 1927 (Shimazu, 1988; Shimazu *et al.*, 2011). (7) 1 (NSMT-Pl 2933) of *A. gotoi*, immature, whole-mounted, ex intestine of *Gymnogobius opperiens* (*Chaenogobius annularis* (the middle-reaches type) and *Chaenogobius urotaenia* of Shimazu (1994)), Oono River, 20 August 1984 (Shimazu, 1988, 1994). One immature and 2 adult specimens (NSMT-Pl 2932, Oono River, 23 August 1983) of Shimazu (1988) were not used. Probably, they had been lost on loan.

Description. Based on specimens (NSMT-Pl 2929–2930) from Lake Kizaki, after Shimazu (1988), modified from the present study (Fig. 5). Body elongate-ovate, slightly tapering posteriorly, fairly small, 2.30–4.54 by 0.80–1.32; forebody 1.27–1.59 long, occupying 35–42% of body length. Eyespot pigment solid or dispersed. Oral sucker 0.32–0.47 by 0.30–0.47. Pharynx 0.15–0.25 in diameter. Esophagus winding,

bifurcating midway between two suckers. Intestines reaching to near posterior extremity of body. Ventral sucker postbifurcal, 0.42–0.61 by 0.40–0.57; sucker width ratio 1 : 1.2–1.3. Testes elliptical, rather small, 0.26–0.47 by 0.24–0.40, almost tandem, usually separated by uterus, in middle third of hindbody. Cirrus pouch claviform, small, 0.16–0.34 by 0.08–0.14, between intestinal bifurcation and ventral sucker. Seminal vesicle tubular, sinuous, in posterior two-thirds of cirrus pouch. Ejaculatory duct short. Genital atrium small. Genital pore immediately postbifurcal. Ovary globular, small, 0.21–0.34 by 0.16–0.27. Seminal receptacle flask-shaped, 0.16–0.32 by 0.12–0.17. Laurer's canal short. Ootype posterolateral to ovary; Mehlis' gland well developed. Uterus between intestines, entering posttesticular region in fully matured specimens more than 3.60 long; metraterm shorter than cirrus pouch. Eggs 80–94 by 46–54 μm. Vitelline follicles dorsal to intestines, distributed usually from bifurcal level to posterior extremity of body, rarely extending to pharyngeal level. Excretory vesicle extending to about midlevel of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. Hasegawa and Ozaki (1926) originally described this species as a new genus and species, *Macrolecithus gotoi*, on the basis of adult specimens found in the intestine of *Misgurnus anguillicaudatus*. They did not specify the locality in Japan. Shimazu (1988) synonymized *Macrolecithus* with *Allocreadium* and made a new combination, *Allocreadium gotoi* (Hasegawa and Ozaki, 1926), for the type species *M. gotoi*. Since Tkach (2008) has recently treated *Macrolecithus* (syn. *Paramacrolecithus* Srivastava and Ghosh, 1967) as a genus *incertae sedis*, the systematic position and validity of *Macrolecithus* will be discussed later again.

Hasegawa and Ozaki (1926) used several whole-mounted and serially sectioned adult specimens for describing *M. gotoi*. The holotype (No. P. 270) was lost (see the Materials and Methods in Shimazu (2013)). Shimazu (1988) doubted that the serially sectioned adult specimen (MPM Coll. No. 30009) belonged to their original specimens. However, I now regard it as the only existing original specimen (a paratype (?)). Yamaguti collected several specimens of *M. gotoi* at Terasho, Shichigo, Komi, Zeze, Lake Biwa, and the unknown locality (see *Material examined*). When Yamaguti (1934, fig. 38) gave measurements of seven whole-mounts and figured the ovarian complex of *M. gotoi*, he did not mention which ones of them he used at that time.

The present specimens agree well in morphology and measurements with the original description by Hasegawa and Ozaki (1926) for *M. gotoi*. The only existing original specimen (MPM Coll. No. 30009) is serially sectioned. The type locality has previously remained unknown. In order to show the adult morphology and type locality, I here designate a neotype for *M. gotoi*, as follows.

Designation of a neotype for Macrolecithus gotoi *Hasegawa and Ozaki*, *1926*, *or now* Allocreadium gotoi (*Hasegawa and Ozaki*, *1926*). Neotype: an adult specimen (NSMT-Pl 2929, 4.04 mm long by 1.32 mm wide, Fig. 1), slightly flattened, whole-mounted, 28 August 1981.

Type host. *Misgurnus anguillicaudatus* (Cantor, 1842) (Cobitidae).

Site of infection. Intestine.

Type locality. Lake Kizaki (36°33′N, 137°50′E) in Oomachi City, Nagano Prefecture, Japan.

Allocreadium gotoi has not as yet been reported from China. However, Okino *et al.* (2004) detected adults of *A. gotoi* in the intestine of *Mi. anguillicaudatus* that had been commercially imported from Zhejiang Province, China, to Japan.

Life cycle. The first intermediate host is *Pisidium nikkoense* Mori, 1938 (or *Pisidium cinereum nikkoense*, *P.* (*P.*) *cinereum nikkoense*) (Bivalvia, Sphaeriidae) (Japanese name: Nikkou-mameshijimi). Shimazu (2002) found sporocysts, mother and daughter rediae, and cercariae in *Pi. nikkoense* (site of infection not determined) collected in the small river at Midori, Iiyama City, Nagano Prefecture (see *Geographical distribution* and *Material examined*; Shimazu, 2007). Cercariae of the ophthalmoxiphidiocercaria [not ophthalmoxiphi-

diocercous] type (with an unarmed body, one pair of eyespots, a simple tail, a stylet, and an I-shaped epithelial excretory vesicle) were produced in the daughter rediae (NSMT-Pl 5215) (Figs. 7–10). Small protuberances were found arranged in a circle on the periphery of the body around the ventral sucker. The penetration gland cells were not observed clearly. Because the same unusual flame cell formula 2[(2 + 3 + 3) + (3 + 3 + 3)] = 34 was determined in both adults of *A. gotoi* and cercariae, Shimazu identified the cercaria as *A. gotoi.* The second intermediate host is unknown. The final hosts are *Misgurnus anguillicaudatus* and *Gnathopogon elongatus elongatus* and possibly *Gymnogobius opperiens*, in the intestine of which adults live (see *Hosts in Japan*).

This cercaria was the first to be reported from sphaeriids in Japan (see Ito, 1964). In order to verify the specific identity between the adult and cercaria in molecular data, adults and cercariae collected by me in the small river at Midori in 2012 were submitted to sequencing the cytochrome *c* oxidase I gene of the mitochondrial DNA (COI mtDNA) and first internal transcribed spacer region of the ribosomal DNA (ITS-1 rDNA). The partial COI gene was not sequenced for either the adults or the cercariae, but the entire ITS-1 region was successfully sequenced for adults (Misako Urabe, 2015, unpublished data). Later, the partial COI gene was successfully sequenced for adults collected by me at the same river in 2015 (Misako Urabe, 2016, unpublished data). I attempted to collect cercariae at the same river three times in 2015 without success.

Allocreadium hasu Ozaki, 1926

(Fig. 6)

Allocreadium hasu Ozaki, 1926: 125, no figure; Yamaguti, 1934: 281–282, no figure; Shimazu, 1988: 9, figs. 4–5 [not 1–2]; Shimazu, Urabe, and Grygier, 2011: 31–33, figs. 36–39.

Allocreadium (*Allocreadium*) *hasu*: Yamaguti, 1954: 69; Yamaguti, 1958: 101; Yamaguti, 1971: 133.

Allocreadium sp.: Shimazu, 1988: 15.

Allocreadium sp. 2: Shimazu, 1999: 71; Shimazu, 2003b: 70.

Hosts in Japan. *Opsariichthys uncirostris uncirostris* (Temminck and Schlegel, 1846) (Cyprinidae) (type host) (Ozaki, 1926; Yamaguti, 1934; Shimazu, 1988; Shimazu *et al.*, 2011; this paper), *Gnathopogon elongatus elongatus* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 1988; Shimazu *et al.*, 2011), *Nipponocypris temminckii* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 1988; this paper), and *Zacco platypus* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 1988; Shimazu *et al.*, 2011).

Site of infection. Intestine.

Geographical distribution. (1) Shiga Prefecture: Lake Biwa basin (Lake Biwa (probably type locality); Imazu-cho, Takashima City; Komatsu (most likely referring to Kitakomatsu, Otsu City); Moriyama City; Omatsu, Minamikomatsu, Otsu City; and Onoe, Kohoku Town) (Yamaguti, 1934; Shimazu, 1988; Shimazu *et al.*, 2011). (2) Hyogo Prefecture: Asago River (Shimazu, 1988). (3) Hiroshima Prefecture: Eno River at Yoshida, Yoshida-cho, Akitakata City; and Saijo River at Ooya, Saijo-cho, Shobara City (Shimazu, 1988; this paper). (4) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City; and Ooyama River at Seiwa Bridge, Ooyama-machi, Hita City (this paper).

Material examined. (1) 17 specimens (Ozaki's Collection, MPM Coll. No. 30006, labeled "*A. hasu* HASU [Lake Biwa]," other data not given, paratypes (?)) of *Allocreadium hasu*, immature, adult, whole-mounted, serially sectioned, ex *Opsariichthys uncirostris uncirostris* (syn. *Opsariichthys uncirostris*), Lake Biwa (Shimazu, 1988; Shimazu *et al.*, 2011). (2) Yamaguti's specimens of *A. hasu*, Lake Biwa basin: 6 (MPM Coll. No. 22287, ex "stomach and small intestine"), adult, whole-mounted, ex intestine of *O. uncirostris uncirostris*, Omatsu, 10 and 17 July 1927; 1 (MPM Coll. No. 22576, labeled "*Allocread. hasu*"), immature, whole-mounted, ex intestine of *O. uncirostris uncirostris*, Lake Biwa, 10 December 1926; 1 (MPM Coll. No.

22569, labeled "*Allocread*. [Moroko]"), adult, whole-mounted, ex intestine of *Gnathopogon elongatus elongatus*, Lake Biwa, 29 July 1927; and 1 (MPM Coll. No. 22576, labeled "*Allocread*. *hasu* [Moroko]"), immature, whole-mounted, ex intestine of *G. elongatus elongatus*, Komatsu (most likely referring to Kitakomatsu), 10 December 1926 (Yamaguti, 1934; Shimazu, 1988; Shimazu *et al.*, 2011). (3) Specimens of *A. hasu*, ex intestine of *O. uncirostris uncirostris*, Lake Biwa basin: 2 (LBM 3-55), adult, whole-mounted, Imazu, 5 May 2000 (Shimazu *et al.*, 2011); 12 (NSMT-Pl 5713), adult, whole-mounted, Moriyama City, 2 May 1992; and 8 (NSMT-Pl 5711–5712), immature, adult, whole-mounted, Omatsu, 30 April 1992, 1 May 1992. One adult specimen (NSMT-Pl 2934, Onoe, now in Kohoku Town, Shiga Prefecture, 6 June 1980) of Shimazu (1988) was not used. Probably, it had been lost on loan. (4) 1 (NSMT-Pl 5714), adult, whole-mounted, ex intestine of *Zacco platypus*, Omatsu, 30 April 1992 (Shimazu *et al.*, 2011). (5) 2 (Yamaguti's Collection, MPM Coll. No. 22286), immature, whole-mounted, ex intestine of *Nipponocypris temminckii* (syn. *Zacco temminckii*), Asago River, 23 March 1932 (Shimazu, 1988). (6) 1 (NSMT-Pl 2936, *Allocreadium* sp. of Shimazu (1988), *Allocreadium* sp. 2 of Shimazu (1999, 2003b)), immature, whole-mounted, ex intestine of *N. temminckii*, Saijo [not Go] River at Hibayama, Saijo Town, now Ooya, Saijo-cho, Shobara City, Hiroshima Prefecture, 31 October 1976 (Shimazu, 1988). (7) Urabe's unpublished specimens: 1, immature, whole-mounted, ex intestine of *N. temminckii*, Ooyama River, 3 November 2003; 1, adult, whole-mounted, ex intestine of *O. uncirostris uncirostris*, Chikugo River, 25 August 2003; and 3 and 1, adult, whole-mounted, ex intestine of *Z. platypus*, Chikugo River, 25 August 2003 and 21 October 2003, respectively.

Description. 1) Based on Ozaki's specimens (MPM Coll. No. 30006), after Shimazu (1988), modified from the present study (Fig. 6). Body elongate-ovate, rapidly attenuated anteriorly in forebody, fairly small, 4.20–5.80 by 1.10–1.80; forebody 0.79–1.11 long, occupying 16–26% of body length. Eyespot pigment fine. Oral sucker 0.31–0.37 by 0.28–0.47. Pharynx 0.16–0.23 by 0.15–0.23. Esophagus bifurcating dorsal to ventral sucker. Intestines ending some distance anterior to posterior extremity of body. Ventral sucker large, 0.43–0.59 by 0.47–0.67; sucker width ratio 1 : 1.4–1.7. Testes deeply indented irregularly, large, 0.55–1.02 by 0.59–1.02, in middle third of hindbody. Cirrus pouch clavate to elliptical, 0.21–0.79 by 0.15–0.47, overlapping ventral sucker (extending to posterior border of ventral sucker in serially sectioned specimens). Seminal vesicle tubular (possibly constricted once in serially sectioned specimens), convoluted, in posterior half to two-thirds of cirrus pouch. Ejaculatory duct fairly long [not short], sinuous. Genital atrium small. Genital pore at midlevel of esophagus. Ovary usually 3-lobed but rarely subglobular, fairly large, 0.36–0.47 by 0.31–0.67. Seminal receptacle flask-shaped, 0.15–0.41 by 0.15–0.39, usually submedian. Laurer's canal short. Ootype postovarian. Uterus between anterior testis and intestinal bifurcation, overlapping intestines; metraterm shorter than cirrus pouch. Eggs 64–78 by 46–56 μm. Vitelline follicles mostly dorsal to intestines, distributed from bifurcal level to posterior extremity of body. Excretory vesicle extending to midlevel of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. Ozaki (1926) described this species, in a preliminary note with no figure, based on adult specimens found in the intestine of *Opsariichthys uncirostris* (now *O. uncirostris uncirostris*), without indicating the type locality in Japan. The holotype (No. P. 231) (Ozaki, 1926) was lost (see the Materials and Methods in Shimazu (2013)). Ozaki's specimens (MPM Coll. No. 30006) were found in *O. uncirostris* from Lake Biwa and identified as *A. hasu* by Ozaki himself. They agree well in morphology and host fish species with Ozaki's original description for *A. hasu*. They are most likely paratypes, which suggests that the type locality is Lake Biwa. However, since the holotype was lost, there is no

conclusive evidence to prove this (Shimazu, 1988; Shimazu *et al.*, 2011).

Later, Yamaguti (1934) described *A. hasu*, with no figure either, from his own specimens found in *O. uncirostris* from Lake Biwa. He seems to have used the six adult specimens (MPM Coll. No. 22287) at least at that time. Shimazu (1988) described *A. hasu* from Ozaki's, Yamaguti's, and his own specimens. Shimazu *et al.* (2011) described *A. hasu* from the specimens from the Lake Biwa basin.

With regard to the shape of the ovary, the ovary is 3-lobed (Ozaki, 1926), ovoid (Yamaguti, 1934), 3-lobed or subglobular (Shimazu, 1988), globular to 3-lobed (Shimazu *et al.*, 2011), and usually 3-lobed but rarely subglobular (this paper). It is apparent from the present examination that, as adult worms grow, the ovary changes its shape from globular to deeply 3-lobed.

Shimazu (1988) reported an immature specimen (NSMT-Pl 2936) as *Allocreadium* sp. (*Allocreadium* sp. 2 of Shimazu (1999, 2003b)) from *Nipponocypris temminckii*. I identify it as *A. hasu*, because the seminal vesicle is weakly constricted once and the testes are large and indented irregularly as in Yamaguti's and Urabe's immature specimens.

One adult specimen (NSMT-Pl 3093) of *A. hasu* of Shimazu (1988) (ex intestine of *Z. platypus*, Eno [not Go] River at Yoshida, now in Yoshida-cho, Akitakata City, Hiroshima Prefecture, 31 October 1976) was not used. Probably, it had been lost on loan.

Life cycle. Not known.

Allocreadium japonicum Ozaki, 1926

(Fig. 11)

Allocreadum japonicum Ozaki, 1926 [*sic*, misspelling of *Allocreadium*]: 124–125, no figure.

Allocreadium japonicum: Yamaguti, 1934: 282, no figure; Shimazu, 1988: 13–14, figs. 10–11; Shimazu, Urabe, and Grygier, 2011: 35–36, figs. 40–43.

Allocreadium (*Allocreadium*) *japonicum*: Yamaguti, 1954: 69; Yamaguti, 1958: 101; Yamaguti, 1971: 133.

Hosts in Japan. Zacco platypus (Temminck and Schlegel, 1846) (Cyprinidae) (type host) (Ozaki, 1926; Yamaguti, 1934; Shimazu, 1988), *Gasterosteus aculeatus leiurus* Linnaeus, 1758 (Gasterosteidae) (Shimazu *et al.*, 2011), *Nipponocypris temminckii* (Temminck and Schlegel, 1846) (Cyprinidae) (Yamaguti, 1934; Shimazu, 1988; this paper), *Phoxinus oxycephalus* (Sauvage and Dabry de Thiersant, 1874) (Cyprinidae) (Shimazu *et al.*, 2011; this paper), and *Tribolodon brandtii* (Dybowski, 1872) (Shimazu, 1988; this paper).

Site of infection. Intestine.

Geographical distribution. (1) Tokyo: Tama River and Shinkawa River (?) (Shimazu, 1988; this paper). (2) Shiga Prefecture: Lake Biwa basin (Lake Biwa; Amano River at Samegai, Maibara City; Momose, Momose-gyoko Fishing Port, Chinai, Makino-cho, Takashima City; and Nyuu River at Shiori, Maibara City) (Yamaguti, 1934; Shimazu, 1988; Shimazu *et al.*, 2011).

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

Material examined. (1) 14 specimens (Ozaki's Collection, MPM Coll. No. 30007, labeled "*Allocreadium* HAYA [Tama River]," other data not given) of *Allocreadium japonicum*, immature, adult, whole-mounted, serially sectioned, ex Haya (see below), Tama River, Tokyo (?) (Shimazu, 1988). (2) 3 (Ozaki's Collection, MPM Coll. No. 30008, labeled "MARUTA [Shinkawa]," other data not given) of *A. japonicum*, adult, whole-mounted, ex *Tribolodon brandtii* (syn. *Tribolodon taczanowskii* Steindachner, 1881), Shinkawa River (?), Tokyo (?) (Shimazu, 1988). (3) Yamaguti's specimens of *A. japonicum*, Lake Biwa: 2 (MPM Coll. No. 22285), adult, whole-mounted, ex intestine of *Zacco platypus*, 7 July 1927; 3 (MPM Coll. No. 22285, labeled "*Allocead.*"), immature, adult, ex intestine of *Z. platypus*, 10 July 1927; and 1 (MPM Coll. No. 22577), adult, whole-mounted, ex intestine of *Nipponocypris temminckii* (syn. *Zacco temminckii*), 7 July 1927 (Yamaguti, 1934; Shimazu, 1988; Shimazu *et al.*, 2011). (4) 1 (LBM 8-18) of *A. japonicum*, adult, whole-mounted, ex intestine of *Gasterosteus aculeatus*

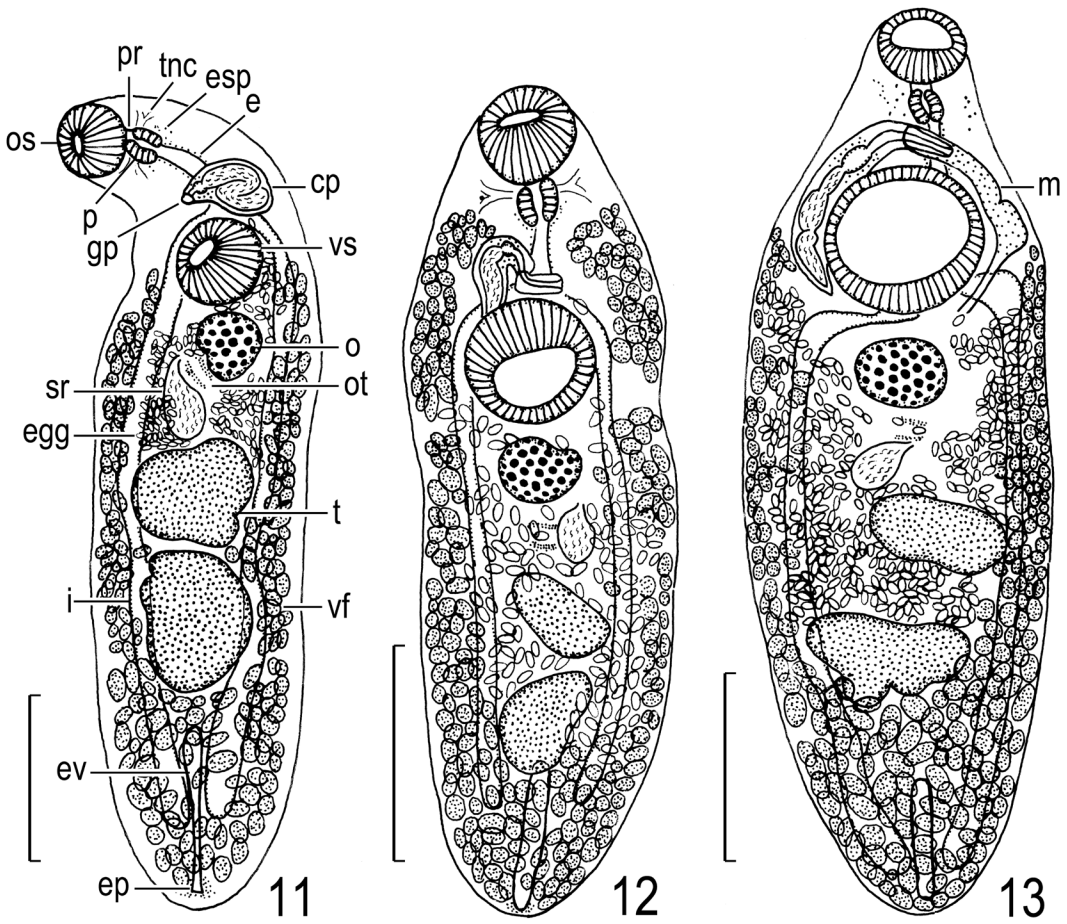


Fig. 11. *Allocreadium japonicum*, adult (MPM Coll. No. 30007) found in intestine of Haya (*Tribolodon hakonensis* [?]), entire body, ventral view. Scale bar: 1 mm.

Fig. 12. *Allocreadium shinanoense*, holotype (NSMT-Pl 5227), adult found in intestine of *Phoxinus steindachneri*, entire body, ventral view. Scale bar: 1 mm.

Fig. 13. *Allocreadium tamoroko*, holotype (NSMT-Pl 5858), adult found in intestine of *Gnathopogon elongatus elongatus*, entire body, ventral view. Scale bar: 1 mm.

leiurus, Amano River, 10 May 1998 (Shimazu *et al.*, 2011). (5) 5 (LBM 8-25) of *A. japonicum*, adult, whole-mounted, ex intestine of *Phoxinus oxycephalus* (syn. *Rhynchocypris oxycephalus*), Nyuu River, 26 April 2001 (Shimazu *et al.*, 2011). (6) 1 (LBM 8-54) of *A. japonicum*, adult, whole-mounted, ex intestine of *Z. platypus*, Momose, 24 November 2007 (Shimazu *et al.*, 2011).

Description. Based on Ozaki's specimens (MPM Coll. No. 30007), after Shimazu (1988), modified from the present study (Fig. 11). Body elongate-oval, fairly small, 4.00–5.40 by 0.86–1.35; forebody 1.03–1.27 long, occupying 24–30% of body length. Eyespot pigment solid or dispersed. Oral sucker 0.31–0.39 by 0.33–0.41 (missing in 2 of 7 specimens). Pharynx 0.15–0.22 by 0.15–0.23. Esophagus bifurcating dorsally to anterior half of ventral sucker. Intestines ending at near posterior extremity of body. Ventral sucker 0.39–0.57 by 0.39–0.55; sucker width ratio 1 : 1.3–1.4. Testes weakly to deeply indented irregularly, large, 0.51–0.86 by 0.35–0.79, almost contiguous, in middle third of hind-

body. Cirrus pouch clavate, 0.27–0.63 by 0.17–0.30, anterior to or overlapping ventral sucker. Seminal vesicle S-shaped, in posterior two-thirds of [not filling] cirrus pouch. Ejaculatory short, duct slightly undulating. Genital atrium fairly large. Genital pore at midlevel of esophagus. Ovary elliptical to weakly 3-lobed, small, 0.39–0.59 by 0.23–0.47, median. Laurer's canal short. Seminal receptacle flask-shaped, 0.19–0.39 by 0.19–0.31. Ootype postovarian. Uterus usually between anterior testis and ventral sucker, rarely extending to posterior testis, slightly overlapping intestines; metraterm shorter than cirrus pouch. Eggs 80–84 by 44–50 μm. Vitelline follicles distributed from about bifurcal level to posterior extremity of body, mostly dorsal to intestines. Excretory vesicle extending to anterior third of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. Ozaki (1926) described this species, in a preliminary note with no figure, based on adult specimens found in the intestine of *Zacco platypus*, without indicating the type locality in Japan. The holotype (No. P. 226) was lost (see the Materials and Methods in Shimazu (2013)).

Because Ozaki reexamined his specimens at his disposal for Peters (Peters, 1957), he must have still possessed some specimens of *A. japonicum* then. Ozaki's Collection today includes the specimens of *Allocreadium* (MPM Coll. Nos. 30006, 30007, and 30008) found in the Hasu (see *A. hasu* above), Haya, and Maruta, respectively. The checklist (Shimazu, 1995) does not include the last specimens.

Ozaki's specimens (MPM Coll. No. 30007) were found in the Haya from the Tama River in [Tokyo (?)]. The question is whether the current scientific name of the Haya is *Z. platypus*. It is either *Z. platypus* or *Tribolodon hakonensis* (Shimazu, 1988). However, local people have traditionally called *T. hakonensis* Haya around the Tama River (Fisheries Cooperative Association of Tamagawa in Fuchu, personal communication, 2011). Ozaki (1926) described the excretory vesicle as reaching anteriorly to the posterior testis in *A. japonicum*. However, the excretory vesicle ends at the anterior third of the post-testicular region in the specimens. As mentioned above, the holotype was lost, the labels are incomplete, the scientific name of the Haya is unknown, and the specimens are different from Ozaki's original description of *A. japonicum* in the anterior extent of the excretory vesicle. In conclusion, it remains unsolved as to whether the specimens (MPM Coll. Nos. 30007) are part of Ozaki's (1926) original specimens of *A. japonicum* from *Z. platypus*, and so the identification of them as *A. japonicum* is provisional. The excretory vesicle does not reach the posterior testis in the others of the present specimens, either (Shimazu, 1988; Shimazu *et al.*, 2011). Accordingly, the identification of them as *A. japonicum* is also provisional. The records of *A. japonicum* by Wang (1984) and Wang *et al.* (1985) from Fujian Province, China, also need validation. I was unsuccessful in obtaining any specimens of *Allocreadium* from 36 individuals of *Z. platypus* and 4 of *T. hakonensis* collected in the Tama River at Fuchu City, Tokyo, on 13 August 2011.

Ozaki found no eyespot pigment in the specimens of *A. japonicum* reexamined except in one "doubtful" specimen (Peters, 1957). Peters (1957) considered that Ozaki's species *A. japonicum* consisted of two genera. One of them was an opecoelid genus owing to the absence of the eyespot pigment and the presence of the 3-lobed ovary. Shimazu (1988) did not agree with him. Eyespot pigment was solid or dispersed in the present specimens.

What are morphological differences between *A. japonicum* and *A. hasu*? Ozaki (1926) seems to have separated *A. japonicum* from *A. hasu* by the testes being smaller and more weakly notched, the vitelline follicles being larger and of irregular shape, and the excretory vesicle being longer and reaching to the posterior testis (see also Shimazu, 1988). Yamaguti (1934) merely stated that *A. japonicum* differed from *A. hasu* in the size of the body, characters of the testes, and extent of the excretory vesicle. The above-mentioned differences are slight, and future studies may demonstrate that *A. japonicum* and *A. hasu*

are conspecific (Shimazu, 1988).

Life cycle. Not known.

Allocreadium shinanoense Shimazu, 2003

(Fig. 12)

Allocreadium shinanoense Shimazu, 2003a: 119–120, figs. 1–3.

Host in Japan. *Phoxinus steindachneri* Sauvage, 1883 (Cyprinidae) (type host) (Shimazu, 2003a; this paper).

Site of infection. Intestine.

Geographical distribution. Nagano Prefecture: Hiroi River (type locality) at Kotobuki, Iiyama City (Shimazu, 2003a).

Material examined. 2 specimens (NSMT-Pl 5227, holotype and 1 paratype) of *Allocreadium shinanoense*, adult, whole-mounted, ex intestine of *Phoxinus steindachneri* (syn. *Rhynchocypris lagowskii steindachneri*), Hiroi River, 12 June 1999 (Shimazu, 2003a).

Description. After Shimazu (2003a), modified from the present study (Fig. 12). Body elongate, fairly small, 3.74–3.80 by 1.16–1.20 (holotype 3.74 by 1.16); forebody 1.27–1.30 long, occupying 33–34% of body length. Eyespot pigment solid. Oral sucker 0.38–0.41 by 0.41–0.42. Pharynx 0.17–0.19 by 0.18–0.19. Esophagus bifurcating immediately anterior to ventral sucker. Intestines ending some distance anterior to posterior extremity of body. Ventral sucker 0.55–0.57 by 0.53–0.57; sucker width ratio 1 : 1.3. Testes elliptical, somewhat irregular in outline, fairly small, 0.35–0.55 by 0.26–0.44, slightly oblique, slightly separated by uterus, in middle third of hindbody. Cirrus pouch claviform, 0.39–0.51 by 0.13–0.14, anterior to ventral sucker, slightly overlapping it posteriorly. Seminal vesicle claviform, 0.34–0.48 by 0.11, in posterior two-thirds of cirrus pouch. Ejaculatory duct fairly long, everted. Genital atrium small. Genital pore immediately anterior to intestinal bifurcation. Ovary globular, somewhat irregular in outline, fairly small, 0.27–0.33 by 0.33–0.39 [not 0.39–0.33]. Seminal receptacle ovate, 0.23–0.27 by 0.13–0.16, sinistrally submedian. Laurer's canal short. Ootype postovarian. Uterus between midlevel of posterior testis and cirrus pouch, overlapping intestines; metraterm shorter than cirrus pouch. Eggs 88–96 by 58–64 μm. Vitelline follicles distributed from level of pharynx to posterior extremity of body. Excretory vesicle reaching to posterior testis; excretory pore posterodorsal.

Remarks. This species and *A. aburahaya* (see above) were obtained from their respective individuals of *Phoxinus steindachneri* from the Hiroi River on 12 June 1999 (Shimazu, 2003a). These two species are considered to be specific to the same fish species, *P. steindachneri*, but very rare in the Hiroi River. The ootype (Shimazu, 2003a, fig. 3) should have been vesicular.

Allocreadium aburahaya and *A. shinanoense* are somewhat similar to *Allocreadium elongatum* (Park, 1939) (syn. *Macrolecithus elongatus* Park, 1939) and *Allocreadium phoxinusi* (Park, 1939) (syn. *Macrolecithus phoxinusi* [*sic*] Park, 1939), respectively, both parasitic in *Rhynchocypris lagowskii* (Dybowski, 1869) (syn. *Phoxinus lagowskii*) from Sensen, North Korea (Park, 1939; Shimazu, 2003a). It is desirable that these four species be morphologically and molecularly compared closely.

Life cycle. Not known.

Allocreadium tamoroko Shimazu and Urabe, 2013

(Fig. 13)

Allocreadium tamoroko Shimazu and Urabe, 2013: 70, figs. 1–2.

Host in Japan. *Gnathopogon elongatus elongatus* (Temminck and Schlegel, 1846) (Cyprinidae) (type host) (Shimazu and Urabe, 2013).

Site of infection. Intestine (Shimazu and Urabe, 2013).

Geographical distribution. Shiga Prefecture: Kayao River at Nakano, Otsu City (Shimazu and Urabe, 2013).

Material examined. 2 specimens (NSMT-Pl 5858, holotype and 1 paratype) of *A. tamoroko*,

adult, whole-mounted, ex intestine of *G. elongatus elongatus*, Kayao River, 1 May 2009 (Shimazu and Urabe, 2013).

Description. After Shimazu and Urabe (2013), modified from the present study (Fig. 13). Body elongate, fairly small, 4.71–4.73 by 1.59–1.63 (holotype 4.73 by 1.59); forebody rapidly tapering anteriorly, 1.11–1.19 long, occupying 23–25% of body length. Eyespot pigment fine. Position of transverse nerve commissure not confirmed. Oral sucker 0.36–0.42 by 0.46–0.47. Pharynx 0.20–0.23 by 0.15–0.16. Esophagus bifurcating at posterior border of ventral sucker. Intestines ending near posterior extremity of body. Ventral sucker large, 0.78–0.80 by 0.82–0.84; sucker width ratio 1 : 1.8. Testes weakly indented irregularly, large, 0.35–0.51 by 0.57–0.84, slightly oblique, separated by uterus, in middle third of hindbody. Cirrus pouch clavate, large, 0.84–1.27 by 0.17–0.22, extending backward to posterior border of ventral sucker. Seminal vesicle sinuous, in posterior half of cirrus pouch. Ejaculatory duct long, slightly everted into metraterm in the holotype. Genital atrium small. Genital pore shifted a little to right or left of median line of body, opening near pharynx in the holotype, not clearly observed (possibly in contact with anterior border of ventral sucker) in the paratype. Ovary elliptical to globular, fairly small, 0.35–0.38 by 0.44–0.47, median. Laurer's canal short. Seminal receptacle flask-shaped, 0.32 by 0.23–0.25. Ootype between ovary and seminal receptacle. Uterus between posterior testis and ventral sucker, overlapping intestines; metraterm clavate, large, almost as long as cirrus pouch, internally warty. Eggs 71–83 by 44–59 μm. Vitelline follicles distributed from midlevel of ventral sucker (or slightly anterior to intestinal bifurcation) to posterior extremity of body, dorsal to intestines. Excretory vesicle extending to midlevel of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. This species is characterized by a long esophagus reaching to the posterior border of the ventral sucker, a large ventral sucker with the sucker width ratio of 1 : 1.8, a large cirrus pouch extending posteriorly to the posterior border of the ventral sucker, and a large internally warty metraterm reaching to the posterior border of the ventral sucker (Shimazu and Urabe, 2013).

Allocreadium tosai Shimazu, 1988

(Fig. 14)

Allocreadium sp.: Seki, 1975b: 13, table 1.
Allocreadium transversale (not of (Rudolphi, 1802) Odhner, 1901): Shimazu, 1981: 17, 19, figs. 8–10.
Allocreadium tosai Shimazu, 1988: 15–16, figs. 12–14; Shimazu, 1994; 70, fig. 4.

Hosts in Japan. *Tribolodon hakonensis* (Günther, 1877) (Cyprinidae) (type host) (Shimazu, 1981, 1988, 1994; this paper), *Oncorhynchus mykiss* (Walbaum, 1792) (Salmonidae) (Shimazu, 1988, 1994; this paper), *Rhynchocypris percnurus* (Pallas, 1814) (Cyprinidae) (Shimazu, 1981, 1988, 1994; this paper), *Salvelinus leucomaenis leucomaenis* (Pallas, 1814) (Salmonidae) (Seki, 1975a, b; Shimazu, 1981, 1988, 1994; this paper), and *Tribolodon sachalinensis* (Nikolskii, 1889) (Shimazu, 1981, 1988, 1994; this paper).

Site of infection. Intestine.

Geographical distribution. Hokkaido: Lake Toro (type locality), Lake Shirarutoro, and Kushiro River at Toro, Shibecha Town (Shimazu, 1981, 1988, 1994; this paper); Lake Panketo at Akan-cho, Kushiro City (Seki, 1975a, b; Shimazu, 1981, 1988, 1994; this paper); and Lake Shikaribetsu at Shikaoi Town (Shimazu, 1988, 1994).

Material examined. (1) 32 specimens (NSMT-Pl 3051, holotype and 31 paratypes) of *Allocreadium tosai*, adult, whole-mounted, ex intestine of *Tribolodon hakonensis*, Lake Toro, 22 July 1984 (Shimazu, 1988). (2) 2 (NSMT-Pl 3053, 2 paratypes, broken) of *A. tosai*, immature, whole-mounted, ex intestine of *T. sachalinensis* (syn. *Tribolodon ezoe* Okada and Ikeda, 1937), Lake Toro, 28 June 1984 (Shimazu, 1988). One immature and 20 adult specimens (NSMT-Pl 3052, 21 paratypes) of Shimazu (1988) were not used. Probably, they had been lost on loan. (3) 4

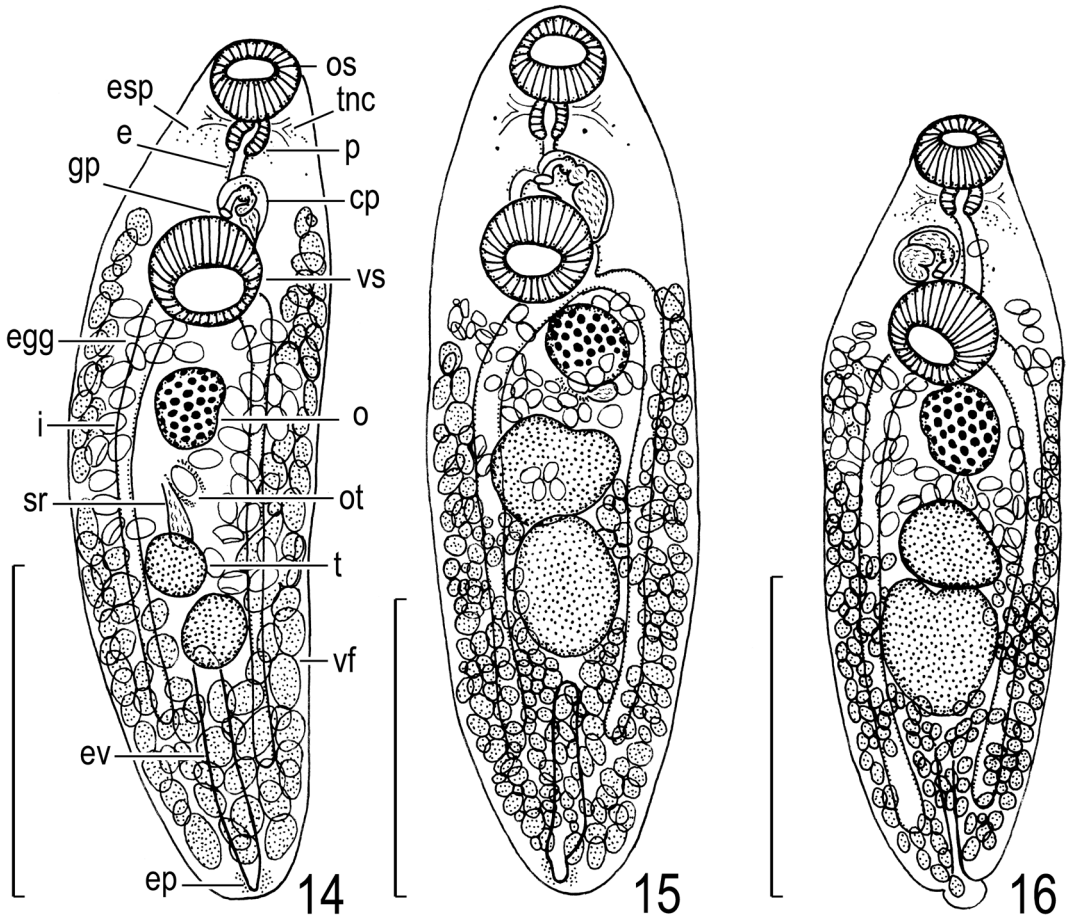


Fig. 14. *Allocreadium tosai*, holotype (NSMT-Pl 3051), adult found in intestine of *Tribolodon hakonensis*, entire body, ventral view. Scale bar: 1 mm.

Fig. 15. *Allocreadium tribolodontis*, holotype (NSMT-Pl 1942), adult found in intestine of *Tribolodon hakonensis*, entire body, ventral view. Scale bar: 1 mm.

Fig. 16. *Allocreadium* sp. of Shimazu (1988), adult (NSMT-Pl 2935) found in intestine of *Gymnogobius opperiens*, entire body, ventral view. Scale bar: 1 mm.

(NSMT-Pl 1843–1844, *A. transversale* of Shimazu (1981), 4 paratypes) of *A. tosai*, adult, whole-mounted, ex intestine of *T. sachalinensis*, Kushiro River, 10 May 1977 (Shimazu, 1981, 1988). (4) 2 (NSMT-Pl 3054, 2 paratypes) of *A. tosai*, adult, whole-mounted, ex intestine of *Rhynchocypris percnurus* (syn. *Moroco percnurus sachalinensis* Berg, 1907), Lake Shirarutoro, 19 September 1981 (Shimazu, 1988).

Description. Based on specimens (NSMT-Pl 3051), after Shimazu (1988), modified from the present study (Fig. 14). Body elongate-ovate, small, 1.80–2.90 by 0.62–0.88 (holotype 2.62 by 0.76); forebody 0.52–0.79 long, occupying 26–32% of body length. Eyespot pigment dispersed. Oral sucker 0.17–0.24 by 0.24–0.27. Pharynx 0.09–0.13 by 0.08–0.12. Esophagus bifurcating just anterior or anterodorsal to ventral sucker. Intestines ending at about midlevel of post-testicular region. Ventral sucker 0.23–0.35 by 0.27–0.34; sucker width ratio 1 : 1.1–1.3. Testes globular to elliptical, small, 0.15–0.27 by 0.15–0.21, oblique, separate or contiguous, in middle third of hindbody. Cirrus pouch ovate, small, 0.12–0.19 by 0.08–0.12, anterior or anterolateral to ventral sucker. Seminal vesicle

sinuous, in posterior half of cirrus pouch. Ejaculatory duct fairly long [not short]. Genital atrium small. Genital pore prebifurcal, usually just anterior to ventral sucker. Ovary elliptical, fairly small, 0.17–0.25 by 0.13–0.19, median or submedian. Seminal receptacle flask-shaped, 0.13–0.19 by 0.05–0.06, submedian. Laurer's canal short. Ootype postovarian. Uterus between posterior testis and ventral sucker, overlapping intestines; metraterm slightly shorter than cirrus pouch. Eggs 92–102 by 60–70 μm. Vitelline follicles distributed from midlevel of esophagus to near posterior extremity of body. Excretory vesicle extending to middle of posterior testis; excretory pore posterodorsal.

Remarks. Shimazu (1981) found four adult specimens (NSMT-Pl 1843–1844) in the intestine of *Tribolodon sachalinensis* and erroneously referred them to a European species, *Allocreadium transversale* (Rudolphi, 1802). Later, Shimazu (1988) obtained additional specimens and proposed a new species, *A. tosai*, for the specimens. This species is distinct from *A. transversale* in that the sucker width ratio is much lower, less than 1 : 1.3 instead of more than 1 : 1.5; the cirrus pouch and genital pore are located prebifurcal instead of postbifurcal; the vitelline follicles extend into the forebody instead of to the bifurcal level; and the excretory vesicle is longer, reaching to the posterior testis instead of saccular and very small (Shimazu, 1988).

Allocreadium tosai most closely resembles *A. brevivitellatum* (see above) in having small testes and a long excretory vesicle extending to the midlevel of the posterior testis, but it differs from the latter in having the vitelline follicles distributed anteriorly to the midlevel of the esophagus instead of to the ovarian level and smaller eggs measuring 84–102 by 60–70 μm instead of 106–130 by 69–80 μm (Shimazu, 1992). The latter has been recorded from only *Rhynchocypris percnurus* of Sarurunto near Lake Toro (Shimazu, 1992).

Seki (1975a, b) reported *Allocreadium* sp. (1975a, pp. 13–14, pl. 1, fig. 6) from the intestine of *Salvelinus leucomaenis leucomaenis* (syn. *S. leucomaenis*) collected in Lake Panketo at Akan, now Akan-cho, Kushiro City, Hokkaido. Reexamining part of Seki's specimens, which were then deposited in the Department of Parasitology, Faculty of Veterinary Medicine, Hokkaido University, Sapporo, Shimazu (1981, 1988) identified the following specimens as *A. tosai*: 2 (No. 379) of *Allocreadium* sp. of Seki (1975a), adult, whole-mounted, ex intestine of *S. leucomaenis leucomaenis*, Lake Panketo; and 13 (No. 374), immature, adult, whole-mounted, ex intestine of *Oncorhynchus mykiss* (syn. *Salmo gairdnei irideus* Gibbons, 1855), Lake Shikaribetsu at Shikaoi Town, Hokkaido, 20 June 1974.

Life cycle. Not known.

Allocreadium tribolodontis Shimazu and Hashimoto, 1999

(Figs. 15)

Allocreadium isoporum (not of (Looss, 1894) Looss, 1900): Shimazu, 1981: 16–17, figs. 5–7; Shimazu, 1988: 10–12, figs. 6–8; Shimazu, 1994: 70, fig. 3.
Allocreadium tribolodontis Shimazu and Hashimoto, 1999: 28–30, figs. 1–4.

Hosts in Japan. *Tribolodon hakonensis* (Günther, 1877) (Cyprinidae) (Hashimoto, 1998; Shimazu and Hashimoto, 1999) and *Tribolodon sachalinensis* (Nikolskii, 1889) (Cyprinidae) (type host) (Shimazu, 1981, 1988, 1994; Shimazu and Hashimoto, 1999; this paper).

Site of infection. Intestine.

Geographical distribution. (1) Hokkaido: Kushiro River (type locality) at Toro, Shibecha Town (Shimazu, 1981, 1988, 1994; Shimazu and Hashimoto, 1999). (2) Iwate Prefecture: Hei River at Kawai, Miyako City (Hashimoto, 1998; Shimazu and Hashimoto, 1999; this paper).

Material examined. (1) 20 specimens (NSMT-Pl 1840–1844, *Allocreadium isoporum* of Shimazu, 1981, 1988, 1994, holotype and 19 paratypes) of *A. tribolodontis*, immature, adult, whole-mounted, ex intestine of *Tribolodon sachalinensis* (syn. *Tribolodon ezoe* Okada and Ikeda, 1937), Kushiro River, 10 May 1977 (Shimazu, 1981, 1988, 1994; Shimazu and Hashimoto, 1999). One immature and 1 adult

specimens (NSMT-Pl 1838–1839, 2 paratypes) of Shimazu (1981, 1988) were not used. Probably, they had been lost on loan. (2) 23 (NSMT-Pl 4576, *Allocreadium* sp. of Hashimoto (1998), 23 paratypes) of *A. tribolodontis*, immature, adult, whole-mounted, ex intestine of *T. hakonensis*, Hei River at Kanioka, Kawai Village, now Kawai, Miyako City, 16 April 1997 (Hashimoto, 1998; Shimazu and Hashimoto, 1999).

Description. Based on specimens (NSMT-Pl 1838–1844) from Hokkaido, after Shimazu (1981, 1988) and Shimazu and Hashimoto (1999), modified from the present study (Fig. 15). Body elongate, small, 2.34–3.10 by 0.80–1.20 (holotype 3.00 by 0.90); forebody 0.63–0.90 long, occupying 25–36% of body length. Eyespot pigment dispersed or not seen. Oral sucker 0.25–0.32 by 0.26–0.32. Pharynx 0.12–0.14 in diameter. Esophagus bifurcating immediately posterior or posterodorsal to ventral sucker. Intestines ending in anterior half of post-testicular region. Ventral sucker 0.31–0.39 by 0.32–0.46; sucker width ratio 1 : 1.1–1.5. Testes round or elliptical, large, 0.24–0.47 by 0.31–0.58, tandem, contiguous, in middle third of hindbody. Cirrus pouch claviform, 0.24–0.35 by 0.08–0.13, anterolateral to ventral sucker, extending posteriorly to middle of ventral sucker. Seminal vesicle bipartite [not tripartite], 0.14–0.25 by 0.06–0.12, in posterior half to two-thirds of cirrus pouch; anterior portion thick-walled, globular, small; posterior one thin-walled, large, usually constricted once weakly. Ejaculatory duct short. Genital atrium small. Genital pore at about midlevel of esophagus, anterior to ventral sucker. Ovary globular, reniform or weakly 3-lobed, fairly small, 0.18–0.31 by 0.24–0.35, median or submedian, immediately posterior to ventral sucker, immediately postbifurcal. Seminal receptacle retort-shaped, 0.12–0.16 by 0.06–0.08, posterolateral to ovary. Laurer's canal short. Ootype posterolateral to ovary. Uterus usually between anterior testis and ventral sucker, occasionally extending posteriorly to posterior testis, overlapping intestines; metraterm much shorter than cirrus pouch [not as long as cirrus pouch]. Eggs 60–80 by 50–60 μm. Vitelline follicles distributed from bifurcal level to posterior extremity of body, ventral and dorsal to intestines. Excretory vesicle extending to anterior half of post-testicular region beyond intestinal ends; excretory pore terminal.

Remarks. Shimazu (1981, 1988) erroneously identified the specimens found in *Tribolodon sachalinensis* (syn. *T. ezoe*) from the Kushiro River as a European species, *Allocreadium isoporum* (Looss, 1894) Looss, 1900 [not Odhner, 1901]. Later, Hashimoto (1998, p. 31, tables 7 and 9) found unidentified specimens of *Allocreadium* in *T. hakonensis* from the Hei River. Shimazu and Hashimoto (1999) described their specimens as a new species, *A. tribolodontis*. This species differs from *A. isoporum* in having a higher sucker width ratio, a larger ovary, and smaller eggs (Shimazu and Hashimoto, 1999). The seminal vesicle is bipartite: the anterior portion is small and thick-walled, and the posterior one is large and thin-walled (Fig. 14). This shape of the seminal vesicle also separates the species from *A. isoporum*.

This freshwater species *A. tribolodontis* has been recorded from eastern Hokkaido and Tohoku (Iwate Prefecture) across the Tsugaru Straits. It is desirable that this record be confirmed from further morphological and molecular studies.

Life cycle. Not known.

***Allocreadium* sp.** of Shimazu (1988)

(Fig. 16)

Allocreadium sp.: Shimazu, 1988: 13, fig. 9; Shimazu, 1994: 70, fig. 5.

Allocreadium sp. 3: Shimazu, 1999: 71; Shimazu, 2003b: 70.

Host in Japan. *Gymnogobius opperiens* Stevenson, 2002 (Gobiidae) (Shimazu, 1988; this paper).

Site of infection. Intestine.

Geographical distribution. Hokkaido: Shumonbetsu River in Mashike Town (Shimazu, 1988; this paper).

Material examined. 1 specimen (NSMT-Pl

2935) of *Allocreadium* sp., adult, whole-mounted, ex intestine of *Gymnogobius opperiens* (*Chaenogobius annularis* Gill, 1859 (the middle-reaches type) of Shimazu, 1988, *Chaenogobius urotaenia* of Shimazu, 1994), Shumonbetsu [not Shubunbetsu] River, 30 July 1984 (Shimazu, 1988).

Description. After Shimazu (1988), modified from the present study (Fig. 16). Body 2.44 by 0.78; forebody 0.68 long, occupying 28% of body length. Eyespot pigment fine. Oral sucker 0.21 by 0.26. Pharynx 0.11 by 0.15. Esophagus bifurcating dorsally to ventral sucker. Intestines ending near posterior extremity of body. Ventral sucker 0.31 by 0.32; sucker width ratio 1 : 1.2. Testes large, 0.26–0.39 by 0.31–0.35. Cirrus pouch globular, 0.22 by 0.19, anterior to ventral sucker. Seminal vesicle convoluted, in posterior two thirds of cirrus pouch. Ejaculatory duct short. Genital atrium small. Genital pore at about midlevel of esophagus. Ovary fairly small, 0.26 in diameter. Seminal receptacle very small, 0.12 by 0.03. Laurer's canal short. Ootype posterodorsal to ovary. Uterus between anterior testis and ventral sucker; metraterm shorter than cirrus pouch. Eggs 74–80 by 50–54 μm. Vitelline follicles distributed from bifurcal level to posterior extremity of body. Excretory vesicle not clearly observed (possibly ending near posterior testis).

Remarks. This specimen is similar to *A. isoporum* of Shimazu, 1988 (or now *A. tribolodontis*) (see above) but different from it in that the cirrus pouch is larger and the seminal vesicle is E-shaped and unipartite.

Life cycle. Not known.

***Allocreadium* sp.** of Shimazu (2005)

(Fig. 17)

Allocreadium sp.: Shimazu, 2005: 140, fig. 4.

Host in Japan. *Tribolodon hakonensis* (Günther, 1877) (Cyprinidae) (Shimazu, 2005).

Site of infection. Intestine.

Geographical distribution. Aomori Prefecture: Lake Ogawara at Kamikita-kita, Tohoku Town (Shimazu, 2005; this paper).

Material examined. 1 specimen (NSMT-Pl 5246) of *Allocreadium* sp., adult, whole-mounted, ex intestine of *Tribolodon hakonensis*, Lake Ogawara at Kamikita Town, now Kamikita-kita, Tohoku Town, 4 September 1997 (Shimazu, 2005).

Description. After Shimazu (2005), modified from the present study (Fig. 17). Body 2.69 by 0.88; forebody 0.83 long, occupying 31% of body length. Eyespot pigment scattered. Oral sucker 0.28 by 0.31. Pharynx 0.15 in diameter. Esophagus bifurcating dorsally to ventral sucker. Intestines ending some distance from posterior extremity of body. Ventral sucker 0.39 by 0.44; sucker width ratio 1 : 1.4. Testes slightly degenerated, small, 0.15–0.29 by 0.15–0.20. Cirrus pouch clavate, 0.21 by 0.10, anterior to ventral sucker. Seminal vesicle bipartite, in posterior half of cirrus pouch; posterior portion larger than anterior one. Ejaculatory duct short. Genital atrium small. Genital pore located at midlevel of esophagus. Ovary fairly small, 0.21 by 0.29. Seminal receptacle retort-shaped, 0.43 by 0.15. Laurer's canal short. Uterus between anterior testis and ventral sucker. Eggs 77–87 by 50–60 μm. Vitelline follicles distributed from bifurcal level to posterior extremity of body. Excretory vesicle extending to midlevel of post-testicular region beyond intestinal ends; excretory pore posterodorsal.

Remarks. This specimen is similar to *A. tribolodontis* (this paper) in having a bipartite seminal vesicle and short excretory vesicle and in the same host fish species (Shimazu, 2005). Additional better-prepared specimens are necessary for definitive species identification.

Life cycle. Not known.

***Allocreadium* sp.** of Shimazu (2008)

(Fig. 18)

Allocreadium sp.: Shimazu, 2008: 48, figs. 3–5.

Host in Japan. *Nipponocypris temminckii* (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu, 2008; this paper).

Site of infection. Intestine.

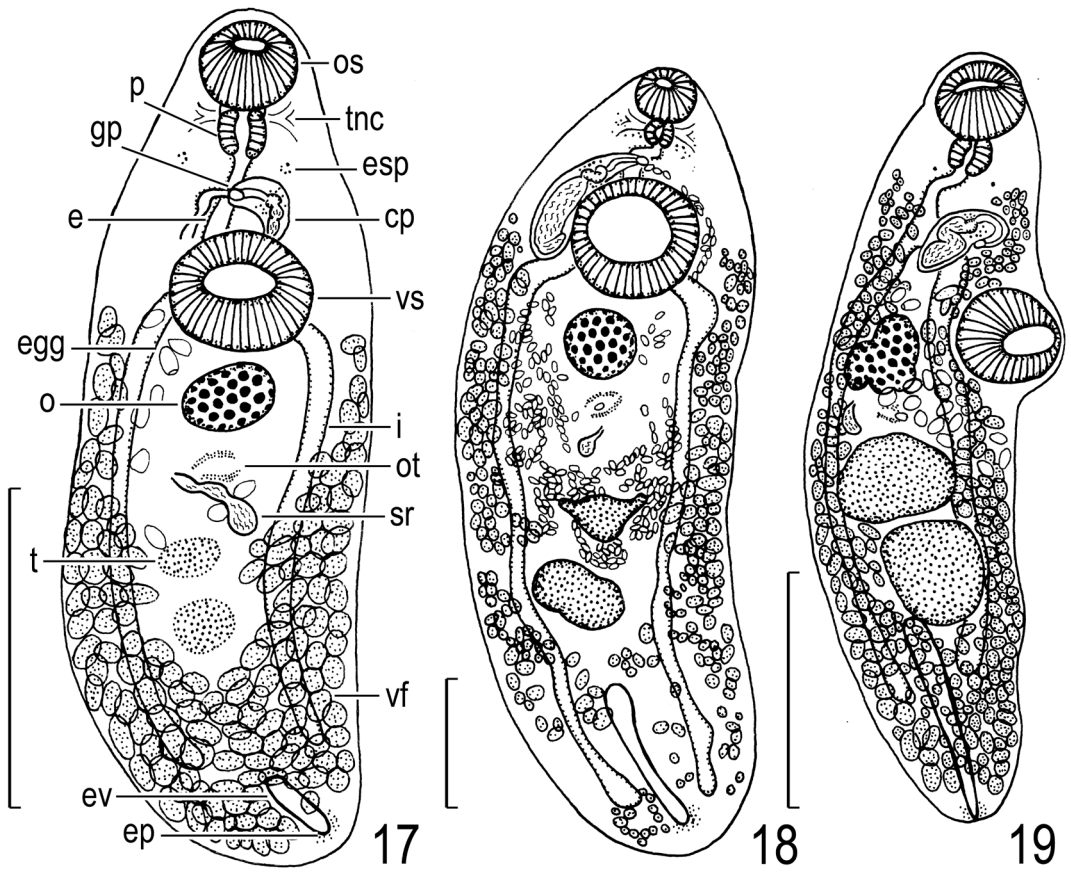


Fig. 17. *Allocreadium* sp. of Shimazu (2005), adult (NSMT-Pl 5246) found in intestine of *Tribolodon hakonensis*, entire body, ventral view. Scale bar: 1 mm.

Fig. 18. *Allocreadium* sp. of Shimazu (2008), adult (NSMT-Pl 5525) found in intestine of *Nipponocypris temminckii*, entire body, ventral view. Scale bar: 1 mm.

Fig. 19. *Allocreadium* sp. of Shimazu *et al.* (2011), adult (LBM 8-26) found in intestine of *Tanakia lanceolata*, entire body, ventral view. Redrawn from Shimazu *et al.* (2011). Scale bar: 1 mm.

Geographical distribution. Tokushima Prefecture: Kaifu River at Yoshino, Kaiyo Town (Shimazu, 2008).

Material examined. 1 specimen (NSMT-Pl 5525) of *Allocreadium* sp., adult, whole-mounted, ex intestine of *Nipponocypris temminckii* (syn. *Zacco temminckii* (Temminck and Schlegel, 1846)), Kaifu River, 11 September 1998 (Shimazu, 2008).

Description. After Shimazu (2008), modified from the present study (Fig. 18). Body elongate, rapidly tapering anterirly, fairly small, 6.40 by 2.19; forebody 1.28 long, occupying 20% of body length. Eyespot pigment present. Oral sucker small, 0.40 by 0.41. Pharynx 0.20 in diameter. Esophagus bifurcating dorsally to ventral sucker. Intestines ending at near posterior extremity of body. Ventral sucker large, 0.94 by 0.98; sucker width ratio 1 : 2.4. Testes apparently atrophied, small, 0.38–0.69 by 0.44–0.55. Cirrus pouch claviform, long, 1.16 by 0.31, extending posteriorly slightly beyond midlevel of ventral sucker. Seminal vesicle sinuous, large, in posterior two-thirds of cirrus pouch, constricted to form small anterior and large posterior portions. Pars prostatica globular, 0.05 by 0.03 [not oblong, 0.02 by 0.01]. Ejaculatory duct long, undulating, slightly everted. Genital atrium small. Genital pore at

about midlevel of esophagus. Ovary fairly small, 0.57 in diameter. Seminal receptacle retort-shaped, 0.16 [not 0.63] by 0.14. Laurer's canal short. Ootype postovarian. Uterus between posterior tests and ventral sucker; metraterm short. Eggs 80–86 by 51–56 μm. Vitelline follicles distributed from bifurcal level to posterior extremity of body. Excretory vesicle extending to about midlevel of post-testicular region; excretory pore posterodorsal.

Remarks. This specimen is somewhat similar to *A. tamoroko* (see above) in having a high sucker width ratio, long esophagus, long cirrus pouch, and short excretory vesicle, and in the anterior extent of the vitelline follicles. However, it is different from the latter in that the sucker width ratio is higher, 1 : 2.4 instead of 1 : 1.8; the metraterm is small and internally smooth instead of large and internally warty; and eggs are larger, 80–86 by 51–56 μm instead of 71–83 by 44–59 μm.

Life cycle. Not known.

***Allocreadium* sp.** of Shimazu, Urabe, and Grygier (2011)

(Fig. 19)

Allocreadium sp.: Shimazu, Urabe, and Grygier, 2011: 36, figs. 44–46.

Host in Japan. Tanakia lanceolata (Temminck and Schlegel, 1846) (Cyprinidae) (Shimazu *et al.*, 2011).

Site of infection. Intestine.

Geographical distribution. Shiga Prefecture: Irrigation canal closely connected to Yogo River at Nishiyama, Kinomoto Town (Shimazu *et al.*, 2011).

Material examined. 2 specimens (LBM 8-26) of *Allocreadium* sp., adult, whole-mounted, ex intestine of *Tanakia lanceolata*, Nishiyama, 26 April 2001 (Shimazu *et al.*, 2011).

Description. After Shimazu *et al.* (2011), modified from the present study (Fig. 19). Body 3.20–3.56 by 0.88–0.94; forebody 1.17–1.20 long, occupying 33–36% of body length. Eyespot pigment solid. Position of transverse nerve commissure not confirmed. Oral sucker 0.32–0.34 by 0.36. Pharynx 0.15–0.17 by 0.19–0.20. Esophagus bifurcating anteriorly to ventral sucker. Intestines ending at near midlevel of post-testicular region. Ventral sucker postbifurcal, 0.41 by 0.43; sucker width ratio 1 : 1.2. Testes elliptical, large, 0.37–0.61 by 0.41–0.50. Cirrus pouch claviform, 0.42–0.43 by 0.15–0.17, anterior to ventral sucker. Seminal vesicle S-shaped, in posterior half of cirrus pouch. Ejaculatory duct fairly long. Genital atrium small. Genital pore shifted to left, about bifurcal. Ovary weakly 3-lobed, fairly large, 0.35–0.36 by 0.28–0.30. Seminal receptacle small, 0.14–0.50 by 0.05. Laurer's canal short. Uterus between posterior margin of anterior testis and cirrus pouch; metraterm as long as cirrus pouch. Eggs 80–89 by 57–62 μm. Vitelline follicles distributed from near posterior margin of pharynx to posterior extremity of body. Excretory vesicle reaching to posterior testis; excretory pore posteroterminal.

Remarks. These specimens are similar to *A. shinanoense* (see above) and *A. japonicum* as described by Ozaki (1926) especially in having a long excretory vesicle reaching to the posterior testis. However, they are different from *A. shinanoense* in having a smaller body, smaller oral and ventral suckers, a lower sucker width ratio, larger testes, a weakly 3-lobed ovary, the uterus extending to the posterior margin of the anterior testis, and smaller eggs; and from *A. japonicum* in having a more posterior ventral sucker, elliptical testes, and a more posterior genital pore (see also Shimazu *et al.*, 2011).

Life cycle. Not known.

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

Allocreadium sp.: Kataoka and Momma, 1934: 59–60, no figure; Shimazu, 1988: 18–19; Shimazu, Urabe, and Grygier, 2011: 89.

Allocreadium sp. 1: Shimazu, 1999: 71; Shimazu, 2003b: 70.

Host in Japan. *Plecoglossus altivelis altivelis* (Temminck and Schlegel, 1846) (syn. *Plecoglossus*

altivelis) (Plecoglossidae) (Kataoka and Momma, 1934).

Site of infection. Intestine.

Geographical distribution. Shiga Prefecture: Lake Biwa (Kataoka and Momma, 1934).

Description. After Kataoka and Momma (1934), modified from the present study. Body ellipsoidal, somewhat elongated, 2.23 by 0.73. Tegument smooth. Oral sucker 0.16 in diameter. Pharynx globular, 0.12 in diameter. Esophagus short, 0.093 long, bifurcating anteriorly to ventral sucker. Ventral sucker larger than oral sucker, 0.296 by 0.31, median, a little anterior to one-sixth of body length. Genital organs occupying "on the whole the entire part behind the ventral sucker." Testes tandem, close to each other, median; anterior testis almost round, 0.41 by 0.44; posterior one irregularly ellipsoidal, 0.59 by 0.38. Situation of cirrus pouch and genital pore and course of uterus and excretory vesicle indistinct. Ovary kidney-shaped, 0.067 by 0.14, pretesticular. Seminal receptacle "elongated gourd-shaped," dorsal to ovary. Egg oval, 73 by 49 μm, operculate. Vitelline follicles comparatively "gross," "not compact," posterior to ventral sucker, along both lateral margins, confluent post-testicularly.

Remarks. Kataoka and Momma (1934) found an adult specimen in the intestine of *Plecoglossus altivelis altivelis* from Lake Biwa. Their brief description of the specimen with no figure lacks anatomical details and positions of the cirrus pouch, genital pore, ovarian complex, and uterus. Accordingly, the specimen cannot be identified even to the family level (see also Shimazu *et al.*, 2011). Kataoka and Momma (1934) mentioned that it closely resembled *Allocreadium oncorhynchi* Eguchi, 1931, or now *Dimerosaccus oncorhynchi* (Eguchi, 1931) (Opecoelidae). However, it has an "elongated gourd-shaped" seminal receptacle (Kataoka and Momma, 1934), and so it cannot be assigned to *D. oncorhynchi* that has no seminal receptacle (Shimazu, 1988, 1999, 2003b; Shimazu *et al.*, 2011). The specimen needs reexamining, but it was most likely lost. No specimen of *Allocreadium* has been found in *Pl. altivelis altivelis* from Lake Biwa since then.

Life cycle. Not known.

Discussion on *Allocreadium*

As shown above, the nine identified and four unidentified species of *Allocreadium* are known from Japanese freshwater fishes. Caira and Bogéa (2005) defined the genital pore as "anterior to ventral sucker, well anterior to, or at level of, intestinal bifurcation" and the uterus as "reaches as far as anterior margin of testes" in their generic diagnosis of *Allocreadium*. However, I included, in *Allocreadium*, not only such species in which the genital pore is prebifurcal or bifurcal and the uterus extends posteriorly to the anterior testis but also species in which the genital pore is postbifurcal and the uterus extends posteriorly to the testicular or post-testicular region. Yamaguti (1971) recognized three subgenera in *Allocreadium*: *Allocreadium* Looss, 1900, *Allocreadioides* "Koval, 1949" [*sic*, should be Yamaguti, 1971], and *Neoallocredium* Akhmerov, 1960. According to Caira and Bogéa (2005), Koval did not propose the subgenus *Allocreadioides*. I do not follow Yamaguti in this paper.

The present review should be considered as offering a framework for testing of taxonomic hypotheses of species of *Allocreadium*, a large digenean group that is predominantly parasitic in cyprinids. Some species in Japan are difficult to study further owing to some inadequate descriptions, some incomplete labels of the existing specimens, and the loss of several critical specimens. Some species in Japan are expected to occur commonly in other parts of East Asia (Russian Far East, Korea, China, and Taiwan), and *vice versa*. At least *A. gotoi* is known in Japan and in Zhejiang Province, China. *Allocreadium aburahaya* and *A. shinanoense* in Japan and *A. elongatum* and *A. phoxinusi* in North Korea should be morphologically and molecularly compared closely. The records of *A. japonicum* from Fujian Province, China, need confirmation. It

seems that some species of *Allocreadium* from the other parts, especially from China, need more detailed descriptions for morphological comparison. It seems likely that molecular approaches will prove important in the future in disentangling the existing taxonomic problems and in elucidating life cycles. The entire ITS-1 and partial COI sequences have been determined for the adult of *A. gotoi* (Misako Urabe, 2015, 2016, unpublished data). Among the Japanese species, the first intermediate host is known in *A. gotoi* only.

The following is a discussion on the systematic position and validity of *Macrolecithus* Hasegawa and Ozaki, 1926. Hasegawa and Ozaki neither gave a generic diagnosis for this genus nor determined its higher taxon (or family) when they created the new genus and species *M. gotoi*. Although they did not compare the genus with *Allocreadium*, these two genera resemble each other. Later, four species were added as new species to the genus: *Macrolecithus elongatus* Park, 1939 and *Macrolecithus phoxinusi* [*sic*] Park, 1939, *Macrolecithus indicus* Gupta and Agrawal, 1967, and *Macrolecithus papilliger* Rees, 1968, from North Korea, India, and UK, respectively (Park, 1939; Gupta and Agrawal, 1967; Rees, 1968). The genital pore is postbifurcal in *M. gotoi* and *M. indicus*, bifurcal in *M. elongatus*, and prebifurcal in *M. phoxinusi* and *M. papilliger*. The uterus extends posteriorly into the post-testicular region in *M. gotoi*, into the testicular region in *M. phoxinusi* and *M. papilliger*, and to the anterior testis in *M. elongatus*. The vitelline follicles are distributed anteriorly to the pharynx in *M. gotoi*, to the esophagus in *M. phoxinusi*, *M. indicus*, and *M. papilliger*, and to the bifurcal level in *M. elongatus*. Although the original description by Hasegawa and Ozaki (1926) suggests that *Macrlecithus* is characterized mainly by the postbifurcal genital pore and the uterus extending into the post-testicular region, its generic characters thus became more uncertain; and it became more similar to *Allocreadium* in the position of the genital pore, posterior extent of the uterus, and anterior distribution of the vitelline follicles.

Macrolecithus was placed in the family Allocreadiidae (Yamaguti, 1934, 1954, 1958; Gupta and Agrawal, 1967; Rees, 1968; Lambert, 1974). Park (1939) stated that the genus was an intermediate form between two families Allocreadiidae and Plagiorchidae Ward, 1917 [*sic*, should be Plagiorchiidae Lühe, 1901]. Later, Yamaguti (1971) allocated the genus to the family Macroderoididae McMullen, 1937 for some reason. However, this allocation is untenable, because *Macroderoides spiniferus* Pearse, 1924 parasitic in the intestine of freshwater fishes has a spinose tegument and xiphidiocercariae (without eyespots) produced in daughter sporocysts in a pulmonate snail (Leigh, 1958) (see *Life cycle* of *A. gotoi* and below).

In the adult stage of *M. gotoi*, the uterus is confined pretesticular in barely matured specimens less than 1.9 mm long. As adult worms grow further, it descends farther into the testicular region in worms more than 2.5 mm long and then even into the post-testicular region in worms more than 4.13 mm long (Hasegawa and Ozaki, 1926; Shimazu, 1988; this paper). In addition to species of *Allocreadium* defined by Caira and Bogéa (2005), some species of *Allocreadium* have the testicular or post-testicular extent of the uterus, *e.g.*, *Allocreadium carparum* Odening, 1959, *Allocreadium dogieli* Koval, 1950, *Allocreadium markewitschi* Koval, 1949, *Allocreadium* (*Allocreadioides*) *hunanense* Lu, 1991, *Allocreadium* (*Allocreadioides*) *multivitellatum* Wang, 1984, *A. transversale*, and *A. tribolodontis* (Odening, 1959; Ergens, 1964; Koval, 1966; Moravec, 1984; Wang, 1984; Lu, 1991; this paper); and some species have the postbifurcal genital pore, *e.g.*, *A. transversale* and *A.* (*A.*) *multivitellatum* (Ergens, 1964; Koval, 1966; Wang, 1984). Wang (1984) assigned *A. multivitellatum* to the subgenus *Allocreadioides* Yamaguti, 1971 (see Lu, 1991). This species has a postbifurcal genital pore and post-testicular extent of the uterus as is the case with *M. gotoi*. Furthermore, Lambert (1974) showed that ophthalmoxiphidiocercariae developed in daughter rediae in a sphaeriid bivalve in *M. papilliger* in

France. Although Lambert determined the flame cell formulae as 2[(3 + 3 + 3 + 3) + (3 + 3 + 3 + 3)] = 48 in the cercaria and 2[(3 + 3) + (3 + 3)] = 24 in the adult, these formulae are questionable. Allocreadiids have cercariae of the same type produced in rediae in sphaeriids and the flame cell formula of 2[(3 + 3 + 3) + (3 + 3 + 3)] = 36 or 2[(4 + 4 + 4) + (4 + 4 + 4)] = 48 (Yamaguti, 1975; Shimazu, 1988; Cribb, 2005; this paper). It is thus difficult to distinguish *Macrolecithus* from *Allocreadium* (see also Shimazu, 1988). Moravec (1984) first transferred *M. papilliger* to *Allocreadium* as *A. papilligerum*, stating that *Macrolecithus* was retained as an independent genus for the time being, because the type specimens of *M. gotoi* were not available to him; however, it was probable that further studies would prove identity of this genus with *Allocreadium*. However, Ozaki's Collection included only the one serially sectioned specimen (MPM Coll. No. 30009) (Shimazu, 1988, 1995; this paper). After examining many other specimens of *M. gotoi* from Japan (see *Material examined* above), Shimazu (1988) concluded that *Macrolecithus* was a junior synonym of *Allocreadium* and made the new combination *A. gotoi* for *M. gotoi*. *Allocreadium gotoi* also produces cercariae of the same type in daughter rediae in a sphaeriid bivalve (Shimazu, 2002; see *Life cycle* above), which supports Shimazu's (1988) conclusion. I do not consider it appropriate to treat *Macrolecithus* as an independent genus in the family Allocreadiidae.

Key to the species of *Allocreadium* in this paper*

1.1. Genital pore postbifurcal; excretory vesicle not reaching to posterior testis; uterus extending posteriorly to posterior testis ..... *A. gotoi*
1.2. Genital pore bifurcal; excretory vesicle reaching to posterior testis; uterus extending posteriorly to posterior testis ..... *A. shinanoense*
1.3. Genital pore prebifurcal; excretory vesicle reaching to posterior testis or not; uterus extending posteriorly to anterior or posterior testis 2
2.1. Excretory vesicle reaching to posterior testis 3
2.2. Excretory vesicle not reaching to posterior testis 4
3.1. Vitelline follicles distributed anteriorly to prebifurcal level ..... *A. tosai*
3.2. Vitelline follicles not distributed anteriorly to bifurcal level ..... *A. brevivitellatum*
4.1. Seminal vesicle bipartite ..... *A. tribolodontis*
4.2. Seminal vesicle unipartite 5
5.1. Vitelline follicles distributed anteriorly to prebifurcal level ..... *A. tamoroko*
5.2. Vitelline follicles distributed anteriorly to bifurcal level 6
6.1. Testes deeply indented irregularly; ovary globular to distinctly 3-lobed ..... *A. hasu*
6.2. Testes weakly indented irregularly; ovary globular to weakly 3-lobed 7
7.1. Body small, 2.56–2.90 long ..... *A. aburahaya*
7.2. Body fairly small, 4.00–5.40 long ..... *A. japonicum*

* This key excludes the four unidentified species.

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