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Digeneans Parasitic in Freshwater Fishes (Osteichthyes) of Japan. XI. Cryptogonimidae and Heterophyidae

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Abstract This paper reviews two species of digeneans parasitic in freshwater fishes of Japan: *Exorchis oviformis* Kobayashi, 1915 (Trematoda, Digenea, Opisthorchioidea, Cryptogonimidae) and *Pseudexorchis major* (Hasegawa, 1935) (Opisthorchioidea, Heterophyidae). They are described and figured. Their life cycles are summarized. Neotypes are designated for *E. oviformis* and *Exorchis major* Hasegawa, 1935, or now *P. major*. Both were found in the intestine of *Silurus asotus* Linnaeus, 1758 (Siluridae) (type host) collected in Lake Kojima (34°34′N, 133°56′E) (type locality) in Okayama Prefecture, Japan.

Key words: Digenea, Cryptogonimidae, Heterophyidae, *Exorchis*, *Pseudexorchis*, neotypes, freshwater fishes, Japan, review.

Introduction

This is the eleventh paper of a series that reviews adult digeneans (Trematoda) parasitic in freshwater fishes (Osteichthyes) of Japan (Shimazu, 2013). This contribution deals with *Exorchis oviformis* Kobayashi, 1915 in the family Cryptogonimidae Ward, 1917 *sensu* Miller and Cribb (2008) and *Pseudexorchis major* (Hasegawa, 1935) in the family Heterophyidae Leiper, 1909 *sensu* Pearson (2008) both in the superfamily Opisthorchioidea Looss, 1899 *sensu* Bray (2008). They are described and figured. Their life cycles are summarized. Neotypes are designated for *E. oviformis* and *Exorchis major* Hasegawa, 1935, or now *P. major*.

The Introduction, Materials, and Methods for the review were given in the first paper (Shimazu, 2013). Specimens examined in the series are whole-mounted ones unless otherwise stated.

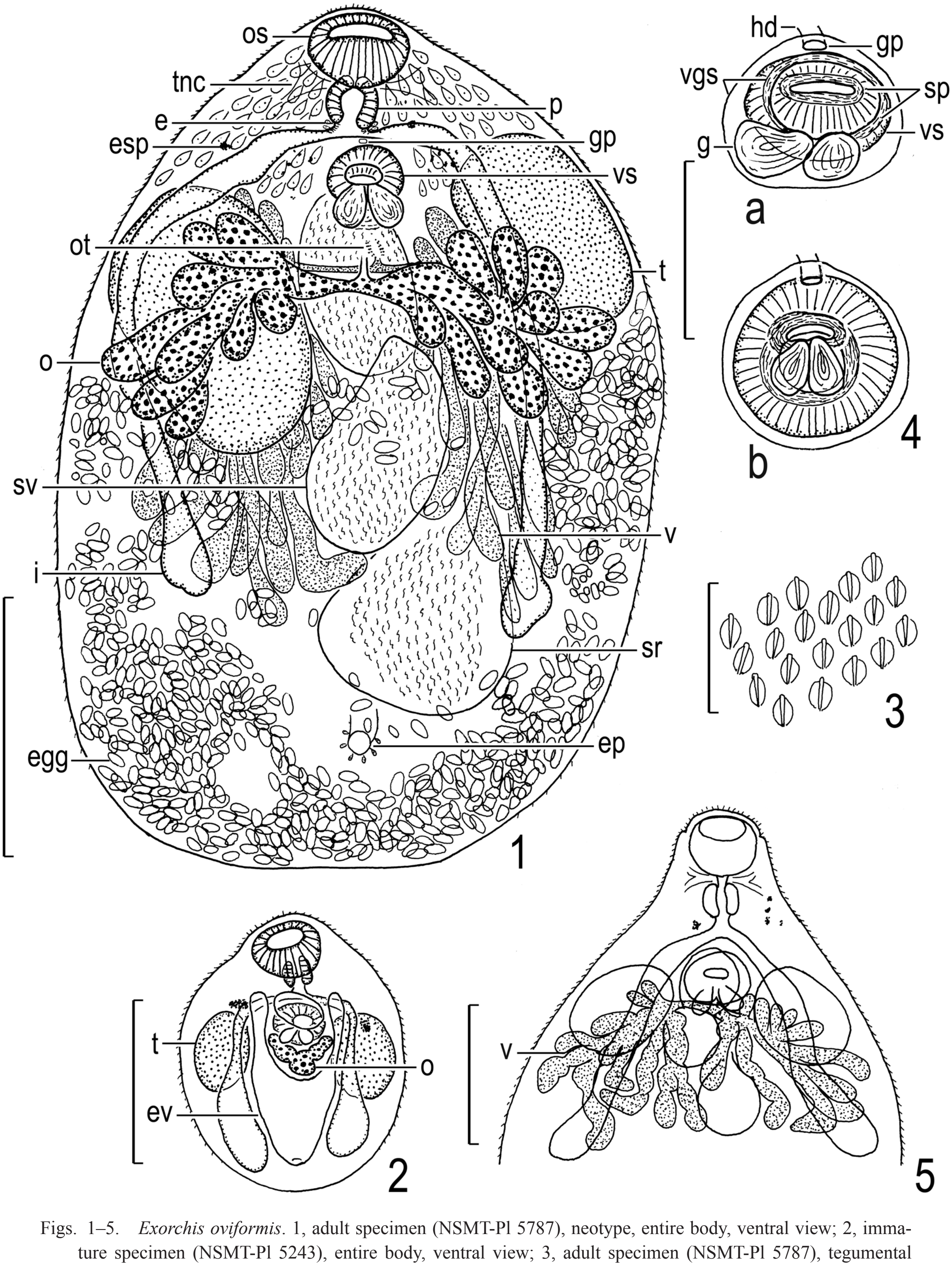
Abbreviations used in the figures. c, cercaria; csd, common sperm duct; cvd, common vitelline duct; dr, daughter redia; e, esophagus; ed, ejaculatory duct; egg, egg in uterus and metraterm; ep, excretory pore; esp, eyespot pigment; ev, excretory vesicle; g, gonotyl; gp, genital pore; hd, hermaphroditic duct; 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 cell; pp, pars prostatica; pr, prepharynx; sd, sperm duct; sp, sphincter; sr, seminal receptacle; sv, seminal vesicle; t, testis; tnc, transverse nerve commissure; u, uterus; v, vitellarium; vd, vitelline duct; vgs, ventrogenital sac; vi, ventral invagination; vs, ventral sucker.

Superfamily Opisthorchioidea Looss, 1899
Family Cryptogonimidae Ward, 1917
Genus *Exorchis* Kobayashi, 1915
Exorchis oviformis Kobayashi, 1915

(Figs. 1–12)

Exorchis oviformis Kobayashi, 1915: 55–56, pl. 2, figs. 7–9; Kobayashi, 1921: 405–407, pl. 26, fig. 5; Takahashi, 1929a: 1926–1927, pl. 2, fig. 6; Hasegawa, 1935b: 1546, 1 plate fig. (not numbered); Yamaguti, 1938: 66; Shimazu, 2005: 145, 147, figs. 15–21.

Metadena oviformis (Kobayashi, 1915): Overstreet, 1971: 158.



Figs. 1–5. *Exorchis oviformis*. 1, adult specimen (NSMT-Pl 5787), neotype, entire body, ventral view; 2, immature specimen (NSMT-Pl 5243), entire body, ventral view; 3, adult specimen (NSMT-Pl 5787), tegumental scales; 4, adult specimens (NSMT-Pl 5243), opened aperture of ventrogenital sac (a) and puckered aperture (b), ventral view; 5, adult specimen (NSMT-Pl 5244), anterior half of body, showing vitellaria, ovary omitted, ventral view. Scale bars: 0.2 mm in Fig. 1; 0.1 mm in Figs. 2 and 5; 0.05 mm in Fig. 4; 0.02 mm in Fig. 3.

Host in Japan. *Silurus asotus* Linnaeus, 1758 (Siluridae) (type host) (Kobayashi, 1915, 1921; Takahashi, 1929a; Hasegawa, 1935b; Yamaguti, 1938, 1942; Shimazu, 2005; this paper).

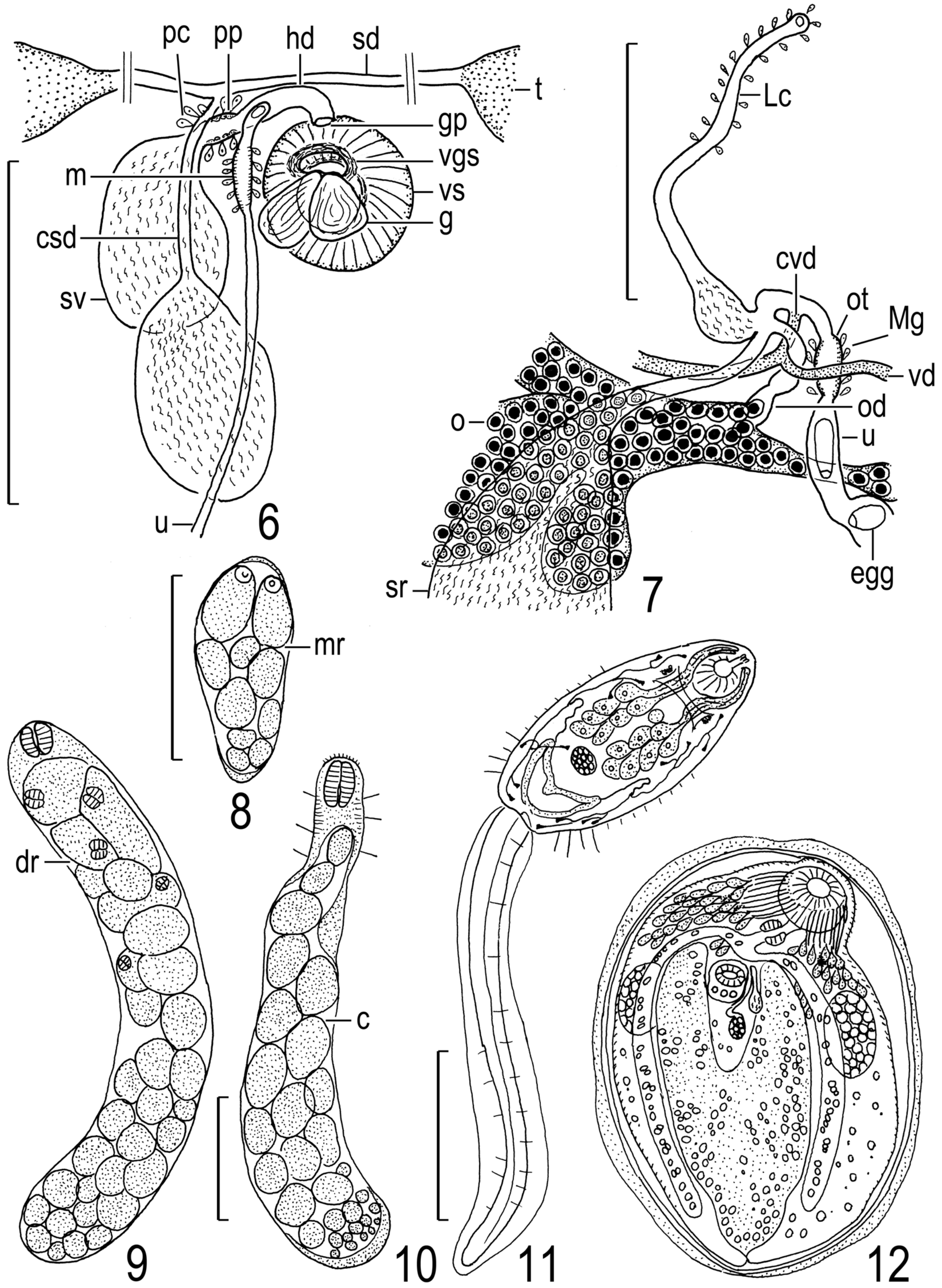
Site of infection. Intestine.

Geographical distribution. (1) Hokkaido: Ishikari River at Ishikari City (Shimazu, 2005). (2) Aomori Prefecture: Lake Ogawara at Asahikita, Tohoku Town (Shimazu, 2005; this paper). (3) Tokyo: Tokyo [exact collecting locality not indicated] (Kobayashi, 1915, 1921). (4) Shiga Prefecture: Lake Biwa [exact collecting locality not indicated] (Kobayashi, 1915). (5) Osaka Prefecture (?): Yodo (Yodo River (?)) (Yamaguti, 1942; Shimazu, 2005). (6) Okayama Prefecture: various places (Kobayashi, 1915, 1921); in the vicinity of Okayama City (Takahashi, 1929a); Nakaune, Minami-ku, Okayama City (Shimazu, 2005; this paper); and Lake Kojima (type locality) (this paper). (7) Fukuoka Prefecture: Okinohata-machi, Yanagawa City (Yamaguti, 1938; Shimazu, 2005; this paper). (8) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (this paper).

In Primorsky Region, Russian Far East (*e.g.*, Besprozvannykh *et al.*, 2000), Korea (*e.g.*, Sohn and Choi, 1997; Baek and Joo, 2009), China (*e.g.*, Komiya and Tajimi, 1940, 1941; Institute of Hydrobiology, Hubei Province (chief ed.), 1973; Wang, 1991), and Vietnam (*e.g.*, Nguyen *et al.*, 2007).

Material examined. (1) 10 specimens (Yamaguti's Collection, MPM Coll. No. 22298) of *Exorchis oviformis*, adult, whole-mounted, ex small intestine [*sic*] of *Silurus asotus* (syn. *Parasilurus asotus*), Okinohata, now Okinohata-machi, Yanagawa City, 24 April 1935 (Yamaguti, 1938; Shimazu, 2005). (2) 1 (Yamaguti's Collection, MPM Coll. No. 22928) of *E. oviformis*, adult, whole-mounted, ex small intestine [*sic*] of *S. asotus*, Yodo (Yodo River (?) in Osaka Prefecture (?)), 12 December 1939 (Yamaguti, 1942; Shimazu, 2005). (3) About 60 (Yamaguti's Collection, MPM Coll. No. 22295-b (number changed), labeled either *Exorchis oviformis* or *Pseudexorchis major*, unpublished) of *E. oviformis*, immature, adult, whole-mounted, ex small intestine [*sic*] of *S. asotus*, Kojo-son, now Nakaune, Minami-ku, Okayama City, 28 September 1935 (Shimazu, 2005). (4) Many (NSMT-Pl 5243) of *E. oviformis*, immature, adult, whole-mounted, ex intestine of *S. asotus*, Lake Ogawara at Kamikita Town, now Asahikita, Tohoku Town, 4 September 1997 (Shimazu, 2005; this paper). (5) Many (NSMT-Pl 5244, hot formalin-fixed) of *E. oviformis*, immature, adult, whole-mounted, ex intestine of *S. asotus*, Ishikari River, 28 June [not November] 1999 (Shimazu, 2005). (6) About 150 (NSMT-Pl 5787–5789, MPM Coll. No. 21220, slightly or strongly flattened or hot formalin-fixed), adult, whole-mounted, ex intestine of *S. asotus*, Lake Kojima, 4 and 11 July 2010. (7) 12 (Urabe's unpublished specimens, labeled *Pseudexorchis major*), adult, whole-mounted, ex intestine of *S. asotus*, Chikugo River, 25 August 2003.

Description. Based on adult specimens (MPM Coll. Nos. 22295-b, 21220; NSMT-Pl 5243, 5244, 5787–5789); 10 specimens (NSMT-Pl 5787, slightly flattened) measured (Figs. 1–7). Body ovate, very small, 0.43–0.70 by 0.33–0.63; forebody 0.11–0.20 long, occupying 21–31% of body length. Tegument covered with scales; scales elliptical to rhombic, each with longitudinal keel-like ridge, diminishing in size and becoming sparser posteriorly, not seen on posteriormost part of body and ventrogenital sac. Eyespot pigment usually solid, in dorsal parenchyma of forebody. Cephalic gland cells numerous, large, filling forebody, each emptying at periphery of body wall over oral sucker (not illustrated; see Fig. 12). Body pigmentation absent. Transverse nerve commissure dorsal to prepharynx. Oral sucker almost globular, small, 0.06–0.10 by 0.07–0.12, anteroventral, embedded half in body wall. Prepharynx very short. Pharynx oval, 0.04–0.06 by 0.03–0.06. Esophagus very short, bifurcating anterior to ventral sucker, surrounded by small gland cells. Intestines extending posteriorly in ventral parenchyma, ending blindly at some distance from posterior extremity of body. Ven-



Figs. 6–7. *Exorchis oviformis* (continued). 6, adult specimen (NSMT-Pl 5243), ventral sucker, ventrogenital sac, gonotyls, male genital organs, and terminal genitalia, ventral view; 7, adult specimen (NSMT-Pl 5787), ovarian complex, dorsal view. Scale bars: 0.1 mm.

Figs. 8–12. *E. oviformis* (continued), life cycle. 8, sporocyst; 9; mother redia (scale not given); 10, daughter redia; 11, cercaria; 12, encysted metacercaria (scale not given). Figs. 8 and 10–12, redrawn from Komiya and Tajimi (1940), modified; Fig. 9, redrawn from Okabe (1936), modified. Scale bars: 0.2 mm in Figs. 8 and 10; 0. 1 mm in Fig. 11.

tral sucker almost globular, small, 0.04–0.06 by 0.05–0.07, with sphincter around aperture, located at about junction of anterior and second fifths of body; sucker width ratio 1 : 0.5–0.8. Ventrogenital sac surrounding ventral sucker, with opened or puckered aperture. Gonotyls two, longitudinal muscular thickenings of posterior wall of ventrogenital sac, sometimes extending anteriorly to close aperture of ventrogenital sac in cooperation with anterior semicircular sphincter around aperture. Testes two, elliptical, large, 0.11–0.20 by 0.06–0.13, symmetrical, submedian, lateral to posterolateral to ventral sucker, posterior to intestinal shoulders, overlapping intestines. Sperm ducts arising from respective anterior ends of testes, possibly running transversely to median line of body, fusing together there to form common sperm duct between esophagus and ventral sucker; common sperm duct possibly running posteriorly to connect with anterior tip of anteroventral protrusion of anterior part of posterior chamber of seminal vesicle. Seminal vesicle bipartite, large, 0.08–0.20 by 0.03–0.07, median, often shifted dextrally or sinistrally, between midlevel of body and ventral sucker, with anteroventral protrusion of anterior part of posterior chamber. Cirrus pouch absent. Pars prostatica small, dorsal or anterior to ventral sucker, anteromedial to seminal vesicle, surrounded by prostatic cells. Ejaculatory duct very short, connecting with metraterm to form hermaphroditic duct; hermaphroditic duct short, opening into ventrogenital sac through median genital pore on its anterior wall. Ovary transversely elongate, much larger than testes, 0.06–0.16 by 0.20–0.37, globular and with two lateral lobes in immature worms (Fig. 2), each lobe irregularly multilobulate in adult worms (Fig. 1), posterior to ventral sucker, ventral to intestines, testes, and seminal vesicle; lobules possibly increasing in number with growth of adult worms. Ovarian complex between ovary and ventral sucker, ventral to seminal vesicle. Seminal receptacle retort-shaped, large, 0.09–0.20 by 0.07–0.11, submedian, rarely reaching to posterior extremity of body. Laurer's canal long, dilated proximally to contain sperm, dextrally or sinistrally submedian, running anteriorly to open dorsally at pharyngeal level. Ootype vesicular, small, surrounded by Mehlis' gland. Uterus much coiled in all available space of postovarian region of body; metraterm short. Eggs numerous, ovate, dark brown, 21–28 by 12–14 μm, with small operculum at attenuated pole, fully embryonated; surface markings on eggshell meshlike, fine. Vitellaria two, large, each multidigitate, symmetrical, slightly separate, in dorsal parenchyma; digits numerous, longitudinally elongate, long, rarely branched, spreading widely between ventral sucker and intestinal ends, overlapping intestines and testes, possibly increasing in number with growth of adult worms. Excretory vesicle Y-shaped; arms extending anteriorly beyond intestinal shoulders; excretory pore usually ventral, some distance away from posterior extremity of body.

Remarks. Kobayashi (1915) established a new genus and species, *Exorchis oviformis*, in a Japanese paper, based on adult specimens found in the intestine of *Silurus asotus* (syn. *Parasilurus asotus*) from Tokyo, Lake Biwa, and various places in Okayama Prefecture. Later, Kobayashi (1921) published an English version, but he removed Lake Biwa from the locality list without mentioning the reason. Kobayashi (1915, 1921) designated neither the holotype nor the type locality for this new species. All of his original specimens were lost (Shimazu, 2013).

Takahashi (1929a) described the female genital organs in adult specimens found in *S. asotus* in the vicinity of Okayama City. Hasegawa (1935b) observed the surface markings of the eggshell [exact collecting locality not indicated]. Yamaguti (1938) gave measurements of adult specimens from Okinohata. Yamaguti (1942) recorded an adult specimen from Yodo. Shimazu (2005) fully described adult specimens from Lake Ogawara and referred to the museum specimens that were available to him at that time.

Miller and Cribb (2008) synonymized *Parametadena* Pan, 1984 with *Exorchis* Kobayashi, 1915 [not 1921] and made a new combination, *Exorchis macrobursae* (Pan, 1984), for *Pa. macrobursae*. The genus *Exorchis* contains five species, *E. oviformis*, *E. macrobursae* (Pan, 1984), *E. multivitellaris* Pan, 1984, *E. ovariolobularis* Cao, 1990, and *E. dongtinghuensis* Zhang, Zuo, Liu, and Zhou, 1993, all parasitic in the intestine of freshwater siluriforms in Asia. *Exorchis oviformis* has been reported from Japan (this paper), Primorsky Region, Russian Far East (*e.g.*, Besprozvannykh *et al.*, 2000), Korea (metacercariae) (Sohn and Choi, 1997; Baek and Joo, 2009), China (*e.g.*, Komiya and Tajimi, 1940, 1941; Institute of Hydrobiology, Hubei Province (chief ed.), 1973; Wang, 1991), and Vietnam (metacercariae) (Nguyen *et al.*, 2007). The four other species are known from China (Pan, 1984; Cao, 1990; Zhang *et al.*, 1993; Tang and Wang, 1997; Ye, 2000). In Vietnam, Nguyen *et al.* (2007) identified metacercariae found in freshwater fishes as *E. oviformis*. Moravec and Sey (1989) described a new species, *Metadena bagarii* (Cryptogonimidae), from a freshwater fish, *Bagarius bagarius* (Siluriformes, Sisoridae). Miller and Cribb (2008) treated *M. bagarii* as a species *incertae sedis*. Further taxonomic studies of *E. oviformis* and *M. bagarii* in Vietnam are needed because they strongly resemble each other in morphology. Sulieman *et al.* (2014) studied the life cycle of *Exorchis mupingensis* Jiang, 2011 in China. This species appeared in Jiang's (2011) unpublished Ph.D. thesis, and so it is unavailable in accordance with Article 9.12 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 2012).

Yamaguti (1971, fig. 567) and Miller and Cribb (2008, fig. 4.36) presented their respective generic diagnoses of *Exorchis* Kobayashi, 1915 [not 1921] apparently based on Kobayashi's (1915, 1921) description and figure of *E. oviformis*. Adult morphology of the genus *Exorchis* (Pan, 1984; Cao, 1990; Zhang *et al.*, 1993; Tang and Wang, 1997; Shimazu, 2005; this paper) differs from that defined by Kobayashi (1915, 1921) and, accordingly, by Yamaguti (1971) and Miller and Cribb (2008) in some generic characters of taxonomic importance, as follows (see also Shimazu, 2005).

1) Ovary. Kobayashi (1915, 1921) described that the ovary was 4- to 5-lobed and much smaller than the testes. Takahashi (1929a, fig. 6) figured a 7-lobed ovary. However, the ovary is much more lobed (or multilobulate) and much larger than the testes in fully matured adult specimens (Shimazu, 2005, figs. 15–16; this paper, Fig. 1). A globular ovary gives off two lateral lobes and is smaller than the testes in immature specimens, in which the vitellaria are still undeveloped (Shimazu, 2005, fig. 17; this paper, Fig. 2).

2) Vitellaria. Kobayashi (1915, 1921) described that the vitellaria were follicular or dendritic in the anterior dorsal part of the body. However, they are two, each being large and multidigitate, with many long longitudinal digits (Shimazu, 2005, figs. 15–16; this paper, Figs. 1 and 5) as in the four other species (Pan, 1984; Cao, 1990; Zhang *et al.*, 1993; Tang and Wang, 1997).

3) Ventrogenital sac and gonotyls. Kobayashi (1915, 1921) merely described that the ventral sucker was deeply depressed. The ventrogenital sac (or body fold of Shimazu (2005)) surrounds the ventral sucker. There are found two gonotyls, or longitudinal muscular thickenings of the posterior wall of the ventrogenital sac (Figs. 1, 2, 4, and 6), though Shimazu (2005, figs. 18–19) described two or three gonotyls. The gonotyls close the aperture of the ventrogenital sac in cooperation with the anterior semicircular sphincter around the aperture of the ventrogenital sac (Fig. 4b and 6). Komiya and Tajimi's (1940, figs. 11 and 13; 1941, fig. 4) figures suggest the presence of the ventrogenital sac and three papillary projections (or gonotyls) in metacercariae (Fig. 12) from China. I failed to observe any gonotyls clearly in whole-mounted excysted metacercariae found in the flesh of *Carassius carassius* [sic] (Cyprinidae) from Yaidu [Yaizu] (9 specimens, MPM Coll. No. 22299, 9 March 1936) and Lake Hamana (1 specimen, MPM Coll. No. 22299, 1 November 1936) in Shizuoka

Prefecture (Yamaguti, 1938); and *Salcocheilichthys variegatus* [sic] from Tutiura [Tsuchiura] (1 specimen, MPM Coll. No. 22299, 8 April 1940) in Ibaraki Prefecture (Yamaguti, 1942); and *Sa. variegatus variegatus* (Temminck and Schlegel, 1846) and *Tanakia limbata* (Temminck and Schlegel, 1846) (Cyprinidae) from the Futatsu River in Yanagawa City, Fukuoka Prefecture (1 specimen each, Urabe's unpublished specimens, 20 August 2002).

4) Seminal vesicle and seminal receptacle. Kobayashi (1915, 1921) described that the seminal vesicle was longitudinally elongated and divided into two unequal parts [elliptical anterior and S-shaped longer posterior chambers] and that the seminal receptacle was absent. He may have mistaken the seminal receptacle for the posterior part of the posterior chamber of the seminal vesicle (see also Yamaguti, 1938). The seminal vesicle is distinctly bipartite. The seminal receptacle is located posterior to the seminal vesicle (Takahashi, 1929a; Yamaguti, 1938; Shimazu, 2005; this paper, Fig. 1).

5) Sperm ducts and common sperm duct. The two sperm ducts arise from the respective anterior borders of the testes (Fig. 6). Although I examined many whole-mounted specimens in the present study, the sperm ducts were too difficult to trace in them. It appeared that the sperm ducts ran transversely to the median line of the body and then fused together to form a common sperm duct, which ran posteriorly to connect with the anterior tip of the anteroventral protrusion of the anterior part of the posterior chamber of the seminal vesicle (Fig. 6). Shimazu (2005, fig. 19) described that the posterior part of the posterior chamber folded double anteriorly [not posteriorly] to connect with the common sperm duct, which is probably erroneous. According to Cao (1990), a long common sperm duct connects with the posterior end of the posterior chamber in *E. ovariolobularis*.

6) Laurer's canal. Kobayashi (1915, 1921) described that Laurer's canal possibly ended blindly. Takahashi (1929a) and Yamaguti (1938) described that it was short and opened near the intestinal bifurcation. However, it is longer and opens dorsally at the pharyngeal level (Shimazu, 2005, fig. 21; this paper, Fig. 7).

7) Eggs. Kobayashi (1915, 1921) described that eggs were 0.04 by 0.02 mm. However, this is obviously erroneous (Yamaguti, 1938). Eggs are 21–28 by 12–14 μm (this paper).

Adult morphology of *E. oviformis* is much better understood now than before. The adult specimens of *E. oviformis* obtained from *S. asotus* in Primorsky Region, Russian Far East (Besprozvannykh *et al.*, 2000), and *S. asotus* and *Pseudobagrus fulvidraco* (Bagridae) in China (Institute of Hydrobiology, Hubei Province (chief ed.), 1973; Wang, 1991) should be carefully reexamined for the morphology (shape and size) of the ovary, vitellaria, seminal vesicle, sperm ducts, seminal receptacle, ventrogenital sac, and gonotyls. Further, it is desirable that the four other species from China be also closely compared with *E. oviformis* in adult morphology.

Overstreet (1971) synonymized *Exorchis* with *Metadena* Linton, 1910 (Cryptogonimidae) and made a new combination, *Metadena oviformis* (Kobayashi, 1915). He stated that the only feature that could be used to separate the species of *Exorchis* [or *E. oviformis*] from those of *Metadena* was the apparent consistently extracecal [or extraintestinal] location of the testes in the former, and he did not consider that of generic magnitude. It is uncertain what adult morphology he recognized at that time *E. oviformis* had, because he neither cited any papers on *E. oviformis* nor referred to any generic characters of *Exorchis* except the extracecal location of the testes. In *Metadena*, the gonotyl is absent or present as a nonmuscular lobe anterior to the ventral sucker instead of posterior, the vitellaria are follicular instead of multidigitate, and species are known from marine fishes instead of freshwater fishes (Miller and Cribb, 2008).

As mentioned above, adults of *E. oviformis* have been found in *Silurus asotus* from rivers, creeks (irrigation canals), and lakes in Hokkaido, Tohoku Region (Aomori Prefecture), Kanto Region (Tokyo), Kinki Region (Shiga (?) and

Osaka (?) Prefectures), Chugoku Region (Okayama Prefecture), and Kyushu Region (Fukuoka and Oita Prefectures) in Japan. Metacercariae (see also above and *Life cycle* below) have also been reported from Tokyo, Lake Biwa in Shiga Prefecture, and various places in Okayama Prefecture (Kobayashi, 1915); Tsuchiura in Ibaraki Prefecture (Yamaguti, 1942) and the Edo River in Tokyo (Kanto Region) (Nihei, 1962); Yaizu and Lake Hamana in Shizuoka Prefecture (Chubu Region) (Yamaguti, 1938); Lake Biwa (Sakai, 1953); Hosorogi Village, now Hosorogi, Awara City, Fukui Prefecture (Chubu Region) (Marugame, 1939); the Yodo River in Osaka Prefecture (Marugame, 1940); various places in Hyogo Prefecture (Kinki Region) (Izumi, 1935); Senoo, now in Minami-ku, Okayama City (Hasegawa, 1934); Okita Village, now Naka-ku, Okayama City (Kuyama, 1938); Naruto City in Tokushima Prefecture (Toyooka, 1965); and Katakasu in Fukuoka City (Okabe, 1936, 1937) and various places in Fukuoka Prefecture (Okabe, 1940; Misako Urabe, 2016, personal communication). The places where the adults and metacercariae were found are almost restricted to coastal areas perhaps owing to the fact that the first intermediate host, *Stenothyra japonica* Kuroda, 1962 (see *Life cycle* below), lives near the sea (Yamaguti, 1938; Shimazu, 2003; Shimazu *et al.*, 2011). Shimazu (2003) and Shimazu *et al.* (2011) questioned the validity of the records of adults (Kobayashi, 1915) and metacercariae (Sakai, 1953) from Lake Biwa, a freshwater lake far away from the sea.

Some of the present adult specimens were found in *S. asotus* from upper reaches of the Chikugo River in Hita City in 2003 (see *Material examined* above). Metacercariae were found in fishes from the lower reaches of this river (Okabe, 1940) and from the Futatsu River (close to the lower reaches of the Chikugo River) in Yanagawa City (see above). Metacercariae were found heavily in *Sarcocheilichthys variegatus variegatus* from this river in 2002 (Urabe, unpublished data). A hydroelectric dam (Yoake Dam) located 10 km from Hita City should have completely prevented fishes including *S. asotus* from migrating up the Chikugo River into Hita City (Yanagi *et al.*, 2010). The reason why the adults were obtained in the Chikugo River at Hita City remains unexplained.

All of Kobayashi's (1915, 1921) original specimens of *E. oviformis* were lost, the type locality has not been designated, and adult morphology is quite different from the original description by Kobayashi (1915, 1921). Therefore, I here designate one of the present specimens as a neotype for *E. oviformis*, as follows.

Neotype of Exorchis oviformis *Kobayashi, 1915*. A whole-mounted adult specimen (NSMT-Pl 5787), slightly flattened, 0.64 mm long by 0.45 mm wide, Fig. 1, 11 July 2010.

Type host. *Silurus asotus* Linnaeus, 1758 (Siluridae).

Site of infection. Intestine.

Type locality. Lake Kojima (34°34′N, 133°56′E) in Okayama Prefecture, Japan.

Life cycle. Okabe (1936, 1937) first discovered first and second intermediate hosts of *E. oviformis* in a creek at Katakasu, now in Hakata-ku, Fukuoka City, Fukuoka Prefecture. Komiya and Tajimi (1940) and Besprozvannykh *et al.* (2000) also studied the life cycle in Shanghai, China, and Primorsky Region, Russian Far East, respectively. The first intermediate hosts were *Stenothyra japonica* (Hirase Ms.) Kuroda, or now *St. japonica* Kuroda, 1962 (Japanese name: Mizugomatsubo) (Gastropoda, Stenothyridae), in Japan, *Stenothyra* sp. in China, and *Stenothyra* (*St.*) *recondita* in Primorsky Region.

Abe (1930) briefly described [Cercaria A] (fig. 1) from a snail collected in Kumamoto Prefecture. This cercaria is also identified as that of *E. oviformis* (Okabe, 1936; Ito, 1964). Abe called the snail [Shou-mamedanishi or Mame-mamedanishi] in Japanese. It may refer to *Gabbia kiusiuensis* (Hirase, 1927) (Bithyniidae), not *St. japonica* as mentioned by Ito (1964) (Shimazu, 2016). The first intermediate host in Korea is said to be *Parafossarulus manchouricus* (Bithyniidae) (Chung *et al.*, 1980). Since *Gabbia* and *Parafossarulus* differ from *Stenothyra* (Stenothyridae) in family level, further taxonomic studies of these host snails in Kumamoto Prefecture and Korea are required.

The sporocyst (Fig. 8) and mother redia (Fig. 9) are known. Pleurolophocercous cercariae (Fig. 11) are produced in daughter rediae (Fig. 10). Okabe (1936) and Komiya and Tajimi (1940) described a 4-pointed stylet in the cercaria, but this is quite possibly a tightly arranged group of penetration spines (Cribb, 1986). The cercaria of *E. dongtinghuensis* has a similar bundle of spines instead of a stylet (Zhang *et al.*, 1993). A small intestine is present in the mother and daughter rediae (Besprozvannykh *et al.*, 2000). The flame cell formula is $2[(2+2)+(2+2)]=16$ in the cercaria (Komiya and Tajimi, 1940) and in the metacercaria (Komiya and Tajimi, 1940, 1941; Besprozvannykh *et al.*, 2000). The caudal excretory canal and two primary excretory pores are present in the anterior part of the cercarial tail (Besprozvannykh *et al.*, 2000) as in the cercariae of *E. dongtinghuensis* (*e.g.*, Zhang *et al.*, 1993) and *E. ovariolobularis* (*e.g.*, Ye, 2000).

Second intermediate hosts are freshwater fishes of several species, in the skin under the scales, gills, and flesh of which metacercariae are found encysted (Fig. 12); and frogs of two species and their tadpoles, in the flesh of which metacercariae are found encysted (*e.g.*, Okabe, 1936, 1937; Komiya, 1965). The final host is *Silurus asotus*, in the intestine of which adults live, in Japan (Kobayashi, 1915, 1921; Yamaguti, 1942; Shimazu, 2005; this paper).

Family Heterophyidae Leiper, 1909

Genus ***Pseudexorchis*** Yamaguti, 1938

Pseudexorchis major (Hasegawa, 1935)

(Figs. 13–21)

Exorchis major Takahashi, 1929b: 2734–2736, 2740–2742, tables 25–28, pls. 8–9, figs. 47–55.

Exorchis major Hasegawa, 1934: 1419–1421, pl. 8, figs. 28–29.

Exorchis major Hasegawa, 1935a: 1193–1199, figs. 1–2; Hasegawa, 1935b: 1546, 1 plate fig. (not numbered).

Pseudexorchis major (Hasegawa, 1935a): Yamaguti, 1938: 67–68, plate fig. 4; Yamaguti, 1954: 152; Yamaguti, 1958: 230; Yamaguti, 1971: 245; Shimazu, 2007: 24–25, figs. 31–34; Shimazu, 2008: 57, fig. 13; Shimazu, Urabe, and Grygier, 2011: 84–85, figs. 116–118.

Pseudexorchis major (Hasegawa, 1934): Yamaguti, 1975: 73; Pearson, 2008: 128.

Hosts in Japan. *Silurus asotus* (Siluridae) (type host) (Hasegawa, 1927, 1935a, b; Takahashi, 1929a, b; Yamaguti, 1938; Shimazu, 2007, 2008; Shimazu *et al.*, 2011; this paper) and *Silurus biwaensis* (Tomoda, 1961) (Shimazu *et al.*, 2011).

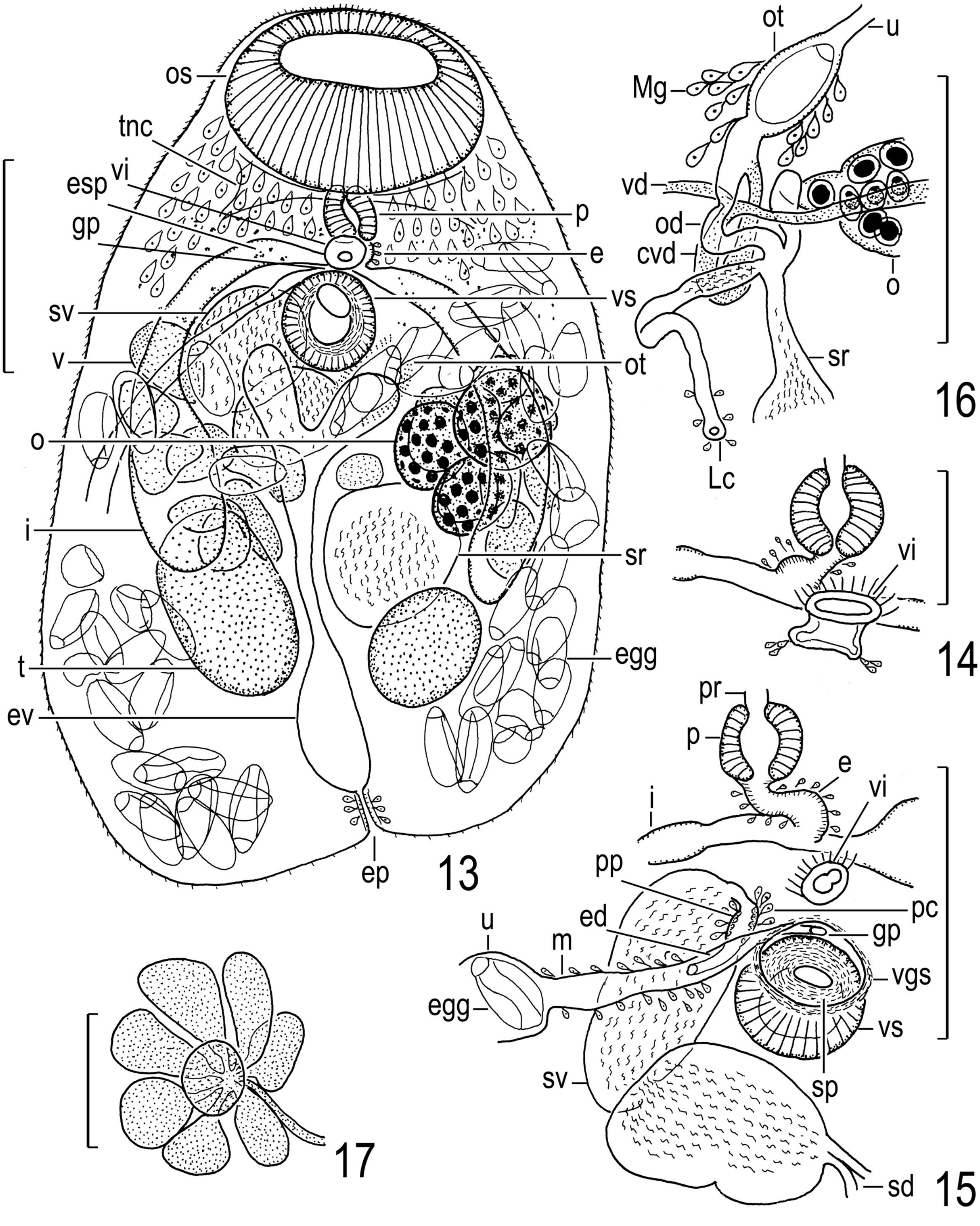
Site of infection. Intestine.

Geographical distribution. (1) Nagano Prefecture: Hiroi River at Kotobuki, Iiyama City; a small river at Kuiseke, Chikuma City; Lake Kizaki and Nogu River in Oomachi City; and Lake Suwa at Suwa City (Shimazu, 2007; this paper). (2) Shiga Prefecture: Lake Biwa basin (Shina-cho, Kusatsu City; Imazu-cho, Takashima City; Momose, Chinai, Makino-cho, Takashima City; Onoe, Kohoku-cho, Nagahama City) (Shimazu *et al.*, 2011; this paper). (3) Hyogo Prefecture: Kobe Market in Kobe City (Hasegawa, 1935a). (4) Okayama Prefecture: in the vicinity of Okayama City (Takahashi, 1929a, b); in the vicinity of Senoo, Minami-ku, Okayama City (Hasegawa, 1935a; this paper); Fujita (a canal flowing in the Sasagase River) and Nakaune, Minami-ku (this paper); Lake Kojima (type locality) (this paper); Lake Kojima at Urayasuminami-machi, Minami-ku (this paper); Kamo River at Tsuchigahara, Tamano City (this paper): and Sasagase River at Hirata, Kita-ku, Okayama City (this paper). (5) Hiroshima Prefecture: Matsuita River at Umaki and Saijo-cho, Higashihiroshima City (this paper). (6) Tokushima Prefecture: a small tributary of Kaifu River at Yoshida and Nishinosawa River at Shihohara, both Kaiyo Town (Shimazu, 2008). (7) Oita Prefecture: Chikugo River at Kobuchi Bridge, Miyoshikobuchi-machi, Hita City (this paper).

In Korea (*e.g.*, Choi *et al.*, 1966).

Material examined. (1) 14 specimens (Yamaguti's Collection, MPM Coll. No. 22295-a (number changed), labeled either *Exorchis oviformis* or *Pseudexorchis major*), adult, whole-mounted, ex small intestine [*sic*] of *Silurus asotus* (syn. *Parasilurus asotus*), Nakaune, 28 September 1935 (Yamaguti, 1938; see also *Material examined* in *Exorchis oviformis*). (2) 22 (Ozaki's Collection, MPM Coll. No. 30211, unpublished), immature, adult, whole-mounted, ex intestine of *S. asotus*, Saijo, now Saijo-cho, 2 June 1941. (3) Many of *P. major*, immature, adult, whole-mounted, ex intestine of *S. asotus*, Nagano Prefecture: (NSMT-Pl 5511), Hiroi River, 17 October 1996; (NSMT-Pl 5512), a small river at Kuiseke, Koshoku City, 22 April 1990; (NSMT-Pl 5502–5507), Lake Kizaki, 5 October 1976, 1 and 14 October 1980, 28 August 1981, 8 September 1981, 24 July 1983; (NSMT-Pl 5508), Nogu River, 1 July 1987; and (NSMT-Pl 5509, 5510), Lake Suwa, 26 May 1975, 13 September 1991, 12 October 1996 (Shimazu, 2007). (4) 27 (NSMT-Pl 5779), adult, whole-mounted, ex intestine of *S. asotus*, Lake Suwa, 26 June 2007. (5) Many of *P. major*, immature, adult, whole-mounted, ex intestine of *S. asotus*, Kaiyo Town: (NSMT-Pl 5558), Kaifu River, 12 September 1998; and (NSMT-Pl 5559), Nishinosawa River, 13 and 15 September 1998 (Shimazu, 2008). (6) 31 (NSMT-Pl 5737, 5738; LBM 8-51) of *P. major*, adult, whole-mounted, ex intestine of *S. asotus*, Lake Biwa basin (Shina-cho; Imazu-cho; Momose; Onoe, Kohoku Town, now in Kohoku-cho, Nagahama City), 11 November 1980, 4 May 1992, 24 November 2007 (Shimazu *et al.*, 2011). (7) About 100 (NSMT-Pl 5790, slightly flattened; 5791, hot formalin-fixed), adult, whole-mounted, ex intestine of *S. asotus*, Lake Kojima (exact collecting locality unknown), 4 and 11 July 2010. (8) Many (MPM Coll. No. 21221), immature, adult, whole-mounted, ex intestine of *S. asotus*, Fujita, 5 May 2012. (9) 5 (MPM Coll. No. 21222), adult, whole-mounted, ex intestine of *S. asotus*, Lake Kojima at Urayasuminami-machi, 12 May 2012. (10) 11 (MPM Coll. No. 21223), adult, whole-mounted, ex intestine of *S. asotus*, Kamo River, 12 May 2012. (11) Many (MPM Coll. No. 21224), immature, adult, whole-mounted, ex intestine of *S. asotus*, Sasagase River, 3 August 2012. (12) 1 (MPM Coll. No. 21225), adult, whole-mounted, ex intestine of *S. asotus*, Nakaune, 8 September 2013. (13) 6 (NSMT-Pl 5780), adult, whole-mounted, ex intestine of *S. asotus*, Matsuita River, 18 June 2009. (14) Many (Urabe's unpublished specimens), immature, adult, whole-mounted, ex intestine of *S. asotus*, Chikugo River, 25 August 2003 (see also *Material examined* in *E. oviformis*).

Description. Based on adult specimens (MPM Coll. Nos. 21221, 22295-a; NSMT-Pl 5502–5507, 5509–5511, 5790, 5791), 10 specimens (NSMP-Pl 5790, slightly flattened) measured (Figs. 13–17). Body broad- to narrow-ovate, anteriorly rounded, posteriorly rotundate, truncate, or cordate, usually symmetrical, sometimes asymmetrical due to posterior elongation caused by uterus packed with eggs, very small, 0.31–0.55 by 0.23–0.34; forebody 0.14–0.20 long, occupying 31–45% of body length. Tegument covered with scales; scales spathulate, diminishing in size and becoming sparser posteriorly, sometimes not seen on posteriormost part of body. Eyespot pigment solid or dispersed in forebody. Cephalic gland cells numerous, around oral sucker in forebody, each emptying at periphery of body wall over oral sucker (not illustrated). Body pigmentation prominent. Ventral invagination invaginated (19–23 by 17–23 μm) (Fig. 14) or everted (Figs. 13 and 15). Transverse nerve commissure dorsal to prepharynx. Oral sucker almost globular, large, 0.08–0.12 by 0.09–0.13, anteroventral, embedded half in body wall. Prepharynx very short. Pharynx elliptical, 0.03–0.04 by 0.02–0.03. Esophagus short, surrounded by small gland cells, bifurcating anterior to ventral sucker. Intestines extending posteriorly in ventral parenchyma, ending blindly at about mid-level of hindbody. Ventral sucker round, small, 0.04–0.05 by 0.04–0.06, slightly posterior to junction of anterior and middle thirds of body; aperture ventral or anteroventral, with thick sphincter; sucker width ratio 1 : 0.4. Ventrogenital sac surrounding ventral sucker. Gonotyl



Figs. 13–17. *Pseudexorchis major*. 13, adult specimen (NSMT-Pl 5790), neotype, entire body, ventral invagination slightly everted, ventral view; 14, adult specimen (NSMT-Pl 5790), invaginated ventral invagination; 15, adult specimen (NSMT-Pl 5790), pharynx, esophagus, intestines (anterior part), slightly everted ventral invagination, ventral sucker, ventrogenital sac, and terminal genitalia, ventral view; 17, adult specimen (MPM Coll. No. 21224), vitellarium consisting of eight follicles, dorsal view. Scale bars: 0.1 mm in Figs. 13 and 15–16; 0.05 mm in Figs. 14 and 17.

absent. Testes globular to elliptical, 0.06–0.10 by 0.06–0.08, almost symmetrical, submedian, posterior to or slightly overlapping intestines. Sperm ducts running transversely, connecting with seminal vesicle; common sperm duct absent. Seminal vesicle bipartite, curved, voluminous, 0.08–0.16 by 0.05–0.09, submedian, immediately posterolateral to ventral sucker on opposite side of ovary. Cirrus pouch absent. Pars prostatica small, anteromedial to seminal vesicle, surrounded by prostatic cells; ejaculatory duct short, connected with metraterm to form hermaphroditic duct; hermaphroditic duct opening into ventrogenital sac through median genital pore on its anterior wall. Ovary 3-lobed, large, 0.07–0.13 by 0.06–0.10, dextrally or sinistrally submedian, about equatorial, between ventral sucker and testis. Ovarian complex posterolateral to ventral sucker, on ovarian side of body. Oviduct short, sometimes dilated to store sperm before giving off Laurer's canal. Seminal receptacle retort-shaped, 0.06–0.12 by 0.03–0.07, posteromedial to ovary. Laurer's canal almost median, short, running posteriorly, sometimes dilated to store sperm, opening dorsally. Ootype vesicular, surrounded by Mehlis' gland, between ventral sucker and ovary. Uterus in ventral parenchyma, first passing transversely from ootype to lateral field on ovarian side of body, descending and then ascending there, then crossing body posteriorly to ventral sucker to opposite side of ovary, sometimes extending posteriorly along median line of body at that time, similarly descending and then ascending there, distributed usually from forebody to post-testicular region of body in both lateral fields in fully mature specimens; metraterm anterior to vitelline follicles, running diagonally on opposite side of ovary, surrounded by small gland cells. Eggs few to numerous, narrow ovate, slightly asymmetrical laterally, dark brown, 32–41 by 16–21 μm, with large domed operculum, fully embryonated when laid; surface markings of eggshell meshlike, prominent. Vitellaria two, each (0.08–0.19 by 0.06–0.12) consisting of eight follicles in dorsal parenchyma, symmetrical, submedian, posterolateral to ventral sucker, at ovarian level. Excretory vesicle Y-shaped, in ventral parenchyma; arms short, not reaching anteriorly to intestinal shoulders; excretory pore posteroterminal.

2) Scanning electron microscopic observation of several adult specimens (fixed in hot 10% formalin, ex intestine of *S. asotus*, Lake Suwa, 26 June 2007). Ventral invagination and genital organs close to each other but distinctly independent from each other (Fig. 18).

Remarks. There is a troublesome nomenclatural problem of the authorship and date of the species name of this species. Takahashi (1929a) described the structure of the ovarian complex of a new species of *Exorchis*. He said that Hasegawa discovered this new species and was to name it *Exorchis major*. Takahashi (1929b) described [daughter (?)] rediae, cercariae, metacercariae, and adults (only the body size) of a digenetic trematode under the species name of *E. major*. He said that Hasegawa discovered this species and preliminarily reported it in 1926. This is evidently his misunderstanding, because Hasegawa's (1926) paper cited by him concerns

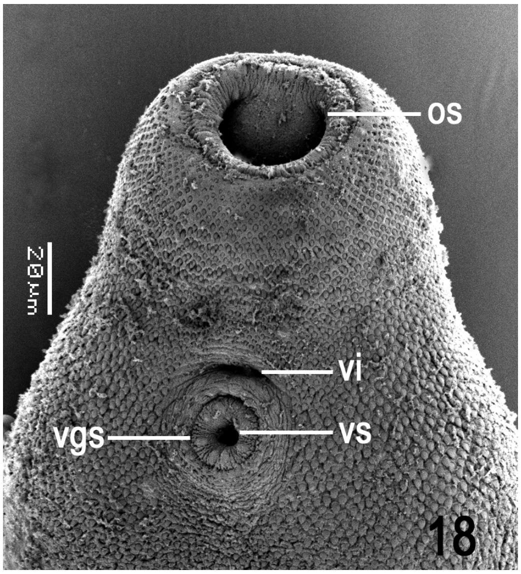


Fig. 18. *Pseudexorchis major* (continued). 5, adult specimen from Lake Suwa, scanning electron micrograph (taken by Toshiaki Kuramochi), anterior part of body, ventral view.

Metagonimus ovatus Yokogawa, 1913. Further, Hasegawa (1934) himself said that he first discovered metacercariae of *E. major* in the scales of *Plecoglossus altivelis* and preliminarily reported them in 1927. However, this new species name does not appear in Hasegawa's (1927) abstract. I consider that at least *E. major* Takahashi, 1929b is available in these cases.

Hasegawa (1927) outlined the life cycle of the digenetic trematode in his abstract. (1) Metacercariae were found encysted in the subcutaneous tissue of the tail, fins, and scales of *Pl. altivelis* (the second intermediate host) from Hyogo Prefecture. (2) Metacercarial cysts were large, the oral sucker was very large, the testes were well developed, and the excretory vesicle was indistinct. (3) Some of them began to form eggs while still encysted in *Pl. altivelis*. (4) The final host was *Silurus asotus* (syn. *Parasilurus asotus*) in Hyogo Prefecture. (5) The first intermediate host experimentally proved to be *Semisulcospira libertina* (see *Life cycle* below). (6) The digenetic trematode represented a new species of *Exorchis* Kobayashi, 1915. Later, Hasegawa (1934) described metacercariae of the digenetic trematode found in the scales of *Pseudorasbora parva* from Senoo under the species name of *Exorchis major*. I consider that *E. major* Hasegawa, 1934 is also available.

Hasegawa (1935a) officially proposed a new species, *Exorchis major*, at last based on adult specimens found in the intestine of *S. asotus*; and described its metacercariae found in *Pl. altivelis*. *Exorchis major* Hasegawa, 1935a is also available. Hasegawa (1935b) observed the surface markings on the eggshell of *E. major*.

Yamaguti (1938) created a new genus, *Pseudexorchis*, to accommodate *E. major* Hasegawa, 1935a, or now *Pseudexorchis major* (Hasegawa, 1935a) (Heterophyidae), as the type and only species. Since then, many subsequent authors (*e.g.*, Ito, 1956, 1964; Komiya, 1965; Yamaguti, 1954, 1958, 1971; Choi *et al.*, 1966; Shimazu, 2007, 2008; Shimazu *et al.*, 2011) have accepted this new combination *P. major* (Hasegawa, 1935a). However, Yamaguti (1975) himself and Pearson (2008) used *P. major* (Hasegawa, 1934). I here accept *P. major* (Hasegawa, 1935a) in order to avoid further confusion about the authorship and date of the species name of the taxon.

Yamaguti (1938) originally assigned *Pseudexorchis* to the family Heterophyidae. Many subsequent authors have followed him (*e.g.*, Yamaguti, 1954; Ito, 1956, 1964; Komiya, 1965; Cribb, 1986; Shimazu, 2007, 2008; Pearson, 2008; Shimazu *et al.*, 2011; this paper). However, Yamaguti (1958, 1971, 1975) placed it in the family Cryptogonimidae. Cribb (1986) returned *Pseudexorchis* to the family Heterophyidae in respect of the anatomy of both adult and cercaria. Pearson (2008) also stated that *Pseudexorchis* was included in the family Heterophyidae, as its cercaria was not cryptogonimid but heterophyid.

I here select some of the morphological characteristics of *P. major*.

1) Ventral invagination (Shimazu, 2007). There is a ventral tubular pit of unknown function between the two suckers. Shimazu (2007) termed it the ventral invagination. It is invaginated or everted (Shimazu, 2007, 2008; Shimazu *et al.*, 2011; this paper, Figs. 13–15, 18). It has no connection with any of the genital organs. Pearson (2008, figs. 5.43–5.44) erroneously described that the copulatory organ (ventral invagination in this paper) was present in the ventrogenital sac. Takahashi (1929b, pl. 9, fig. 55, Pg), Hasegawa (1934, pl. 8, fig. 29, k; 1935a, fig. 1, [genital pore]), and many other subsequent authors (*e.g.*, Yamaguti, 1938, 1971, 1975; Ito, 1956; Choi *et al.*, 1966) misinterpreted it as either the genital pore or the genital atrium. It is absent in *Exorchis oviformis* (see above).

2) Ventrogenital sac. The ventrogenital sac surrounds the ventral sucker. Hasegawa (1935a) merely described that the ventral sucker was completely embedded in the body wall. The hermaphroditic duct opens into the ventrogenital sac through the median genital pore on its anterior wall (Shimazu, 2007, 2008; Shimazu *et al.*, 2011; this paper, Fig. 15). No gonotyl is present in *P. major*.

3) Ovary. The ovary is 3-lobed (Hasegawa. 1935a; Shimazu, 2007, 2008; Shimazu *et al.*, 2011). Pearson (2008, fig. 5.42) erroneously described an elliptical ovary.

4) Vitellaria. The vitellarium is a compact cluster of eight follicles on either side of the body (Fig. 17). Hasegawa (1935a) did not refer to the number of the follicles. Shimazu (2007, 2008) and Shimazu *et al.* (2011) erroneously described seven follicles each. Pearson (2008, fig. 5.42) figured seven and eight follicles.

5) Eggs. Hasegawa (1935a) gave an erroneous egg size (0.0494–0.0572 by 0.026–0.0286 mm) (50–57 by 26–29 μm in Pearson (2008)). The egg size is actually smaller: 32–41 by 16–21 μm (this paper). The eggshell is somewhat asymmetrical laterally and has prominent meshlike markings on the surface (Hasegawa, 1935a, b; this paper).

6) *Situs inversus*. A *situs inversus* (Hasegawa, 1935a), or a transposition, is seen in some of the genital organs. The ovary is dextrally or sinistrally submedian. The ootype complex, seminal receptacle, and proximal part of the uterus are always submedian on the ovarian side of the body; and the seminal vesicle and metraterm are always submedian on the opposite side.

Hasegawa (1927) first found adults of *P. major* in *Silurus asotus* from Hyogo Prefecture. Takahashi (1929a) described the female genital organs in adult specimens found in *S. asotus* from near Okayama City. Takahashi (1929b) gave the body size of 4- and 8-day-old experimental adult specimens (see *Life cycle* below). Hasegawa (1935a) fully described *E. major*, stating that adults were common in *S. asotus* from near Senoo in Okayama City and the Kobe Market in Kobe City, Hyogo Prefecture. Yamaguti (1938, plate fig. 4) only presented a photomicrograph of an adult specimen without mentioning the data. I discovered this adult specimen among those (Yamaguti's Collection, MPM Coll. No. 22295-a) found in *S. asotus* from Kojo-son in Okayama Prefecture (see *Material examined* above). Shimazu (2007, 2008) and Shimazu *et al.* (2011) fully described adult specimens found in *S. asotus* from Nagano and Tokushima Prefectures and *S. asotus* and *S. biwaensis* from Shiga Prefecture, respectively. In addition, cercariae and metacercariae have been reported from various freshwater areas in Japan except Hokkaido (Ito, 1964; Komiya, 1965).

I consider that all of Hasegawa's (1934, 1935a, b) and Takahashi's (1929a, b) specimens of *E. major* were lost, because none of them is deposited in the collection of the Faculty of Medicine (formerly Okayama Igaku Senmon Gakko), Okayama University, Okayama (Toshiki Aji, personal communication, 14 November 2012). Therefore, I here designate one of the present specimens as a neotype of *P. major*, as follows.

Neotype of Exorchis major *Hasegawa*, *1935*, *or now* Pseudexorchis major (*Hasegawa*, *1935*). A whole-mounted adult specimen (NSMT-Pl 5790), slightly flattened, 0.40 mm long by 0.25 mm wide, Fig. 13, 11 July 2010.

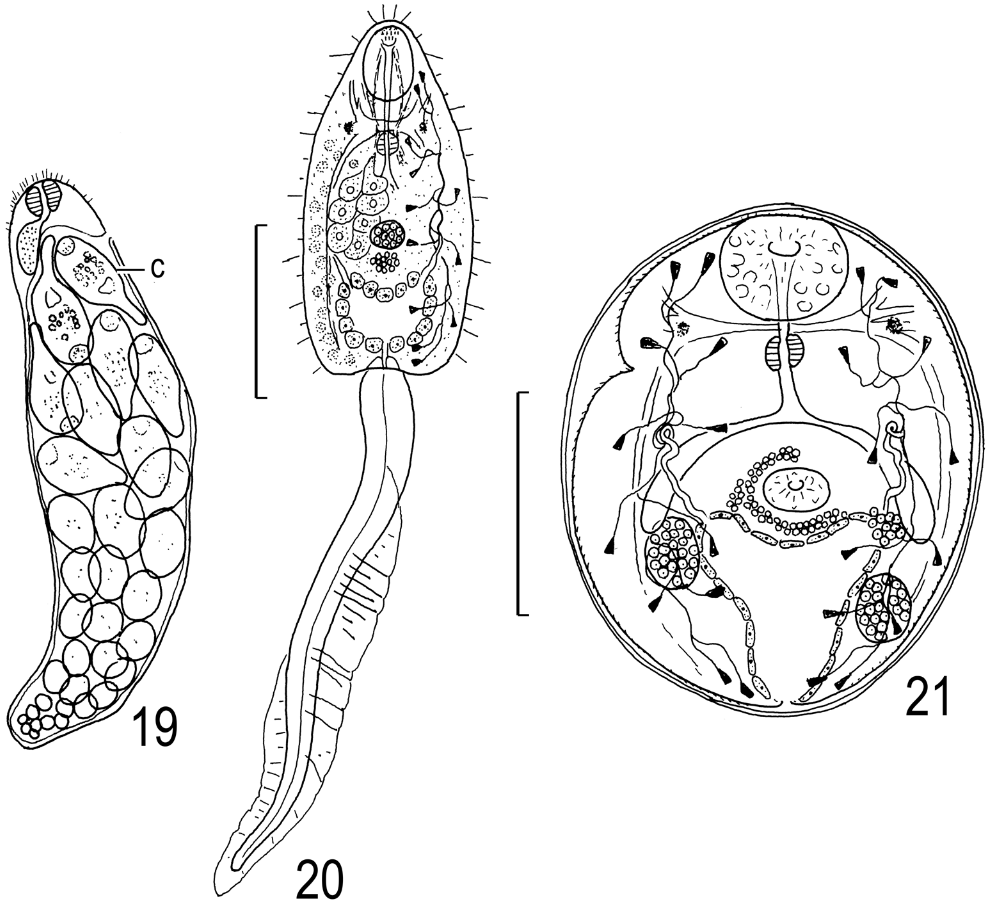
Type host. *Silurus asotus* Linnaeus, 1758 (Siluridae).

Site of infection. Intestine.

Type locality. Lake Kojima (34°34′N, 133°56′E) in Okayama Prefecture, Japan.

Life cycle. As shown above, Hasegawa (1927) first outlined the life cycle of *E. major* (now *P. major*). Takahashi (1929b), Yamaguti (1938), and Ito (1956) also studied the life cycle.

First intermediate hosts are pleurocerid snails, *Semisulcospira libertina* (syn. *Thiara* (*Melania*) *libertina*) (Japanese name: Kawanina) and several other species and subspecies of *Semisulcospira* in Japan and Korea (*e.g.*, Hasegawa, 1927; Takahashi, 1929b; Yamaguti, 1938; Ito, 1956, 1964; Kim *et al.*, 1987; Urabe, 2003; Shimazu, 2007). The range of the snail species reported as the intermediate host is considerably wide. They may need to be further taxonomically studied according to the present-day classification of *Semisulcospira*. It is easy to identify the cercaria of *P. major* correctly according to the description of the cercaria by Ito (1956, 1964). Pleurolophocercous cercariae (Fig. 20) are produced in daughter rediae (Fig. 19). The penetration (or oral) spines of three transverse rows (three in the



Figs. 19–21. *Pseudexorchis major* (continued), life cycle. 19, daughter redia (scale not given); 20, cercaria, ventral view; 21, encysted metacercaria, ventral view. Redrawn from Ito (1956), modified. Scale bars: 0.1 mm in Figs. 20–21.

posterior row) are present instead of a stylet. The flame cell formula in the cercaria and metacercaria is $2[(2+2+2)+(2+2+2)]=24$ (Figs. 20–21). The excretory system in the cercarial tail has not yet been described. Neither the sporocyst nor the mother redia has yet been found.

Second intermediate hosts are freshwater fishes of various species, mainly in the scales, fin rays, and bones of which metacercariae (Fig. 21) are found encysted (*e.g.*, Takahashi, 1929b; Hasegawa, 1927, 1934, 1935a; Yamaguti, 1938; Ito, 1956; Komiya, 1965; Shimazu *et al.*, 2011). Some metacercariae begin to form eggs while still encysted (Hasegawa, 1927, 1934, 1935a). Final hosts in Japan are *Silurus asotus* and *S. biwaensis*, in the intestine of which adults live (*e.g.*, Hasegawa, 1927, 1935a; Takahashi, 1929a, b; Yamaguti, 1938; Shimazu, 2007, 2008; Shimazu *et al.*, 2011; this paper).

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