

***Isoparorchis hypselobagri* (Trematoda: Isoparorchidae) from freshwater fishes in western Japan, with a review of its host-parasite relationships in Japan (1915–2013)**

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Abstract. Specimens of *Isoparorchis hypselobagri* (Billet, 1898) were collected from the following freshwater fishes in western Japan: *Anguilla japonica* (Anguillidae) from Shimane and Ehime prefectures; *Silurus asotus* (Siluridae) from Hiroshima and Yamaguchi prefectures; *Acanthogobius flavimanus* (Gobiidae) from Shimane Prefecture; *Candidia temminckii* (Cyprinidae), *Pungtungia herzi* (Cyprinidae), *Rhinogobius fluvialis* (Gobiidae), and *Rhinogobius* sp. (Gobiidae) from Hiroshima Prefecture. The collection of *I. hypselobagri* from *A. japonica*, *A. flavimanus*, *R. fluvialis*, and *Rhinogobius* sp. represents new host records, and the parasite is reported for the first time from Hiroshima, Yamaguchi, and Ehime prefectures. Host-parasite relationships of *I. hypselobagri* infecting Japanese freshwater fishes are reviewed based on the literature published in 1915–2013.

Key words: *Isoparorchis hypselobagri*, Trematoda, fish parasite, new host records

Introduction

Trematodes of the digenean family Isoparorchidae are endoparasites of freshwater fishes in Asia and Australasia (Gibson, 2002), where *Isoparorchis hypselobagri* (Billet, 1898) has been reported from the Russian Far East (Bykhovskaya-Pavlovskaya & Kulakova, 1987), Japan (Shimazu *et al.*, 2011), China (Chen *et al.*, 1973), Vietnam (Moravec & Sey, 1989), Indonesia (Bovien, 1927), Bangladesh (Chandra, 2006), India (Bhalerao, 1936), Pakistan (Bilquees & Khatoon, 1972), and Australia (Cribb, 1988). Because of its large body size of adult worms (up to over 40 mm) and impacts on fish hosts, much attention has been paid to various aspects of the biology of the species, such as the morphology (e.g.,

Tewari & Pandey, 1989), physiology (e.g., Adak & Manna, 2011), body composition (e.g., Srivastava & Gupta, 1976), occurrence in fishes (e.g., Devaraji & Ranganathan, 1967; Bashirullah, 1972), and pathology (e.g., Mahajan *et al.*, 1979; Li *et al.*, 2002).

During a study of the parasite fauna of freshwater fishes of western Japan, we collected specimens of *I. hypselobagri* in Shimane, Hiroshima, Yamaguchi, and Ehime prefectures. This collection includes new host and prefecture records for the parasite. In Japan, the species has been studied for its morphology and ecology since 1915 when Kobayashi (1915a) first described it. However, many of those studies have been published in Japanese, thus it is difficult for scientists of other countries to fully understand the knowledge of the species reported in Japan. The present paper reports on our findings and, using the literature published between 1915 and 2013, reviews

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the host-parasite relationships of the species infecting Japanese freshwater fishes.

Materials and Methods

Freshwater fishes were collected at various localities in Shimane, Hiroshima, Yamaguchi, and Ehime prefectures, western Japan, in 2008–2013. Fishes were transported alive to the laboratory at Hiroshima University, where they were identified using Nakabo (2002) and examined for parasites. Trematodes were flattened between slide glass and cover-slip, fixed in 70% ethanol, stained in Heidenhain's iron hematoxyline, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam. They were measured for body length (BL, mm) and examined for maturity: worms with and without eggs in the uterus were recorded as mature and immature, respectively. Drawings were made with the aid of a drawing tube. Representative voucher specimens are deposited in the Platyhelminthes (PI) collection housed at the National Museum of Nature and Science (NSMT-PI) in Tsukuba, Ibaraki Prefecture, Japan, and the remaining specimens are retained in the senior author's collection. The scientific and Japanese names of fishes used in this paper are adopted from Nakabo (2013) and the English names of fishes are from Froese & Pauly (2013).

Results and Discussion

Specimens of *I. hypselobagri* were collected from the following fishes in western Japan:

1) *Anguilla japonica* Temminck & Schlegel, 1847 (Anguilliformes: Anguillidae): one immature specimen (6.4 mm BL, site: stomach wall tissue) from the Sozu River, Ainan Town, Ehime Prefecture, on 5 July 2008; four immature specimens (2.3–5.8 mm BL, sites: mesentery and outer surface of air bladder wall, NSMT-PI 6022 [N=1, Fig. 1A]) from Lake Shinji, Izumo City, Shimane Prefecture, on 3 August 2011; and one immature specimen (9.6 mm BL, site: mesentery) from Lake Nakaumi, Matsue City, Shimane Prefecture, on 8 November 2011.

2) *Candidia temminckii* (Temminck & Schlegel, 1846) (Cypriniformes: Cyprinidae): one immature (6.8 mm BL, site: mesentery) and one mature (9.6 mm BL, site: mesentery, NSMT-PI 6023 [N=1]) specimens from the Nukui River, a tributary of the Kurose River, Higashi-Hiroshima City, Hiroshima Prefecture, on 26 and 28 March 2012, respectively.

3) *Pungtungia herzi* Herzenstein, 1892 (Cypriniformes: Cyprinidae): one mature (26.1 mm BL, site: body muscle, NSMT-PI 6024 [N=1, Fig. 2]) and one immature (11.2 mm BL, site: mesentery) specimens from the Nukui River, a tributary of the Kurose River, Higashi-Hiroshima City, Hiroshima Prefecture, on 24 July 2012.

4) *Silurus asotus* Linnaeus, 1758 (Siluriformes: Siluridae): three mature (12.5–20.3 mm BL, site: air bladder) and one immature (3.2 mm BL, body cavity) specimens from the Awano River, Shimonoseki City, Yamaguchi Prefecture, on 22 February 2011; four mature (22.9–45.2 mm BL, site: air bladder, NSMT-PI 6025 [N=1]) and three mature (35.9–40.1 mm BL, site: air bladder) specimens from the Furuko River, a tributary of the Kurose River, Higashi-Hiroshima City, Hiroshima Prefecture, on 21 February and 10 July 2012, respectively.

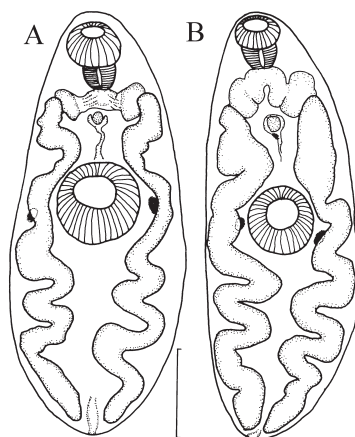


Fig. 1. *Isoparorchis hypselobagri*: A, immature specimen, NSMT-PI 6022, from *Anguilla japonica* in Lake Shinji, Shimane Prefecture; B, immature specimen, NSMT-PI 6026, from *Acanthogobius flavimanus* in Lake Shinji, Shimane Prefecture. Scale bars: 1 mm.

5) *Acanthogobius flavimanus* (Temminck & Schlegel, 1845) (Perciformes: Gobiidae): six immature specimens (2.4–5.3 mm BL, site: body cavity, NSMT-PI 6026 [N=1, Fig. 1B]) from Lake Shinji, Matsue City, Shimane Prefecture, on 8 January 2013.

6) *Rhinogobius fluviatilis* Tanaka, 1925 (= *Rhinogobius* sp. LD of Nakabo [2002]; LD= large-dark type [Anonymous, 1989]) (Perciformes: Gobiidae): one immature (4.2 mm BL, site: liver tissue, NSMT-PI 6027 [N=1]) and three immature (3.3–4.4 mm BL, site: liver tissue, NSMT-PI 6028 [N=1]) specimens from the Furuko River, a tributary of the Kurose River, Higashi-Hiroshima City, Hiroshima Prefecture, on 10 January 2012 and 13 September 2012, respectively.

7) *Rhinogobius* sp. (= *Rhinogobius* sp. OR of Nakabo [2002]; OR=orange type [Anonymous, 1989]) (Perciformes: Gobiidae): one immature

specimen (2.5 mm BL, site: liver tissue, NSMT-PI 6029 [N=1]) from the Furuko River, a tributary of the Kurose River, Higashi-Hiroshima, Hiroshima Prefecture, on 13 September 2012.

Since immature and mature worms of *I. hypselobagri* were well described by Yamashita & Nishida (1955) and Shimazu *et al.* (2011), respectively, and our observation did not add new information on its morphology, no description of the specimens collected is given in this paper. Four species of fishes, *A. japonica*, *A. flavimanus*, *R. fluviatilis*, and *Rhinogobius* sp. (= *Rhinogobius* sp. OR of Nakabo [2002]), are new host records for *I. hypselobagri*. This parasite is herein reported for the first time from Hiroshima, Yamaguchi, and Ehime prefectures in Japan. The fish hosts of *I. hypselobagri* in Japan is listed in Table 1.

There was a taxonomic confusion in *R. fluviatilis* and *Rhinogobius* sp. in Japan. The former species was earlier reported as “*Rhinogobius* sp. LD” (Nakabo, 2002), but Suzuki & Chen (2011) conducted a detailed taxonomic study of gobiids of the genus and concluded that both are identical with each other: thus, *R. fluviatilis* is a current valid name. Although *Rhinogobius* sp. reported in this paper was formerly regarded as “*Rhinogobius* sp. OR” (Nakabo, 2002), the latter has been demonstrated to include several species (Suzuki *et al.*, 2010) and, following Nakabo (2013), *Rhinogobius* sp. is herein used. Future identification of *Rhinogobius* sp. examined in this study, a specimen preserved in 70% ethanol is kept in the junior author’s (M.N.) collection.

Review of the host-parasite relationships of *Isoparorchis hypselobagri* infecting Japanese freshwater fishes

In Japan, this parasite was originally described by Kobayashi (1915a) as *Leptolecithum eurytremum* using mature specimens from the air bladder of *Silurus asotus* (as *Parasilurus asotus*) and *Tachysurus nudiceps* (as *Pseudobagrus aurantiacus*) (see below for the scientific name of this species) and immature specimens from the body cavity of these fishes,

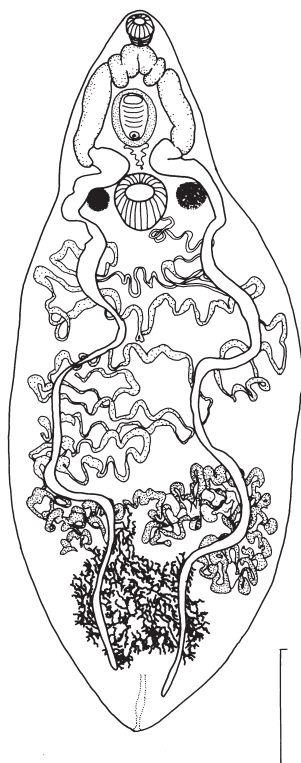


Fig. 2. *Isoparorchis hypselobagri*: mature specimen, NSMT-PI 6024, from *Pungtungia herzi* in the Nukui River, a tributary of the Kurose River, Hiroshima Prefecture. Scale bar: 4 mm.

Table 1. Fish hosts of *Isoparorchis hypselobagri* in Japan, based on the previous and present studies. The classification scheme and scientific and Japanese names of fishes are adopted from Nakabo (2013). If present, English names of fishes are also adopted from Froese & Pauly (2013).

Order	Family	Scientific name	Japanese name	English name	Prefecture	Reference
Anguilliformes	Anguillidae	<i>Anguilla japonica</i>	nihon-unagi	Japanese eel	Shimane, Ehime	present study
Cypriniformes	Cyprinidae	<i>Candidia sieboldii</i> (as <i>Nipponocypris sieboldii</i>)	numamutsu	—*	Shiga	Shimazu <i>et al.</i> (2011)
		<i>Candidia temminckii</i> (as <i>Zacco temminckii</i>)	kawamutsu	dark chub	Nara, Oita, Hiroshima	Sawada & Osako (1969); Kugi & Shiote (1979); present study
		<i>Gnathopogon elongatus elongatus</i>	ta-moroko	—	Nagano, Shiga	Yamaguti (1938); Shimazu <i>et al.</i> (2011)
		<i>Hemibarbus barbus</i>	nigoi	—	Tokyo	Suzuki <i>et al.</i> (1967); Kamegai <i>et al.</i> (1972)
		<i>Opsariichthys platypus</i> (as <i>Zacco platypus</i>)	oikawa	freshwater minnow	Oita	Okabe (1940); Kugi & Shiote (1979)
		<i>Pseudogobio esocinus esocinus</i> (as <i>Pseudogobio esocinus</i>)	kamatsuka	—	Gunma, Tokyo, Shiga	Nihei <i>et al.</i> (1964); Suzuki <i>et al.</i> (1967); Shimazu <i>et al.</i> (2011)
		<i>Pungtungia herzi</i>	mugitsuku	—	Shiga, Hiroshima, Fukuoka	Kifune (1978); Shimazu <i>et al.</i> (2011); present study
		<i>Sarcocheilichthys variegatus microoculus</i> (as <i>Sarcocheilichthys variegatus</i>)	biwa-higai	—	Ibaraki	Yamaguti (1934)
		<i>Tanakia lanceolata</i>	yari-tanago	—	Shiga	Shimazu <i>et al.</i> (2011)
		<i>Tribolodon hakonensis</i> (as <i>Richardsonius hakonensis</i> , <i>Leuciscus hakonensis</i>)	ugui	big-scaled redfin	Ibaraki	Kobayashi (1915a, 1921); Yamaguti (1934)
Siluriformes	Bagridae	<i>Tachysurus nudiceps</i> (as <i>Pseudobagrus aurantiacus</i>)	gigi	—	Ibaraki, Chiba, Shiga, Okayama	Kobayashi (1915a, 1915b, 1921)
	Siluridae	<i>Silurus biwaensis</i>	biwako-ō-namazu	Eurasian catfish	Shiga	Shimazu <i>et al.</i> (2011)
		<i>Silurus asotus</i> (as <i>Parasilurus asotus</i>)	namazu	Amur catfish	Ibaraki, Gunma, Chiba, Tokyo, Nagano, Shiga, Kyoto, Okayama, Hiroshima, Yamaguchi, Miyazaki	Kobayashi (1915a, 1915b, 1921); Yamaguti (1934); Nihei <i>et al.</i> (1964); Suzuki <i>et al.</i> (1967); Iwata <i>et al.</i> (2007); Shimazu (2007); Shimazu <i>et al.</i> (2011); present study
Salmoniformes	Osmeridae	<i>Hypomesus nipponensis</i> (as <i>Hypomesus olidus</i>)	wakasagi	Japanese smelt	Not clear**	Kobayashi (1915a, 1921)
Perciformes	Centrarchidae	<i>Lepomis macrochirus</i>	burūgiru	bluegill	Shiga	Shimazu <i>et al.</i> (2011)
		<i>Micropterus salmoides</i>	burakku-basu	largemouth black bass	Shiga	Grygier (2004); Shimazu <i>et al.</i> (2011)
	Cottidae	<i>Cottus reinii</i>	utsusemi-kajika	—	Shiga	Shimazu <i>et al.</i> (2011)
	Odontobutidae	<i>Odontobutis obscura</i> (as <i>Mogruna obscura</i>)	donko	—	Not reported	Yamaguti (1934)
	Gobiidae	<i>Acanthogobius flavimanus</i>	mahaze	yellowfin goby	Shimane	present study
		<i>Gymnogobius urotaenia</i> (as <i>Chaenogobius macrognathos</i>)**	ukigori	—	Nagano, Shiga	Yamaguti (1938); Shimazu <i>et al.</i> (2011)
		<i>Rhinogobius fluviatilis</i>	ō-yoshinobori	—	Hiroshima	present study
		<i>Rhinogobius</i> sp. BW	biwa-yoshinobori	—	Shiga	Shimazu <i>et al.</i> (2011)
		<i>Rhinogobius</i> sp.****	—	—	Hiroshima	present study
		<i>Tridentiger brevispinis</i>	numa-chichibu	—	Shiga, Kyoto	Shimazu & Urabe (2005); Shimazu <i>et al.</i> (2011)
		<i>Channa argus</i> (as <i>Ophicephalus argus</i>)	kamuruchī	snakehead	Ibaraki, Chiba, Shiga, Shimane, Kochi, Kumamoto	Yamashita & Nishida (1955); Komatsu & Matsumura (1963); Suzuki <i>et al.</i> (1967); Uehara (1972); Shimazu <i>et al.</i> (2011)
	Channidae					

*: No English name.

**: Kobayashi (1915a, 1921) collected the infected fishes of four species, including *H. nipponensis*, in Okayama, Chiba, Ibaraki, and Shiga prefectures but did not indicate the sampling locality of the parasite.

***: See Shimazu (2007) for the scientific name of this gobiid.

****: This is identical with "*Rhinogobius* sp. OR" (Nakabo, 2002).

Hypomesus nipponensis (as *H. olidus*) and *Tribolodon hakonensis* (as *Richardosonius hakuensis*) collected in Okayama, Chiba, Ibaraki, and Shiga prefectures. Kobayashi (1915a) did not designate a type locality nor a type host for this parasite. As the original description was published in Japanese, its English version was later published (Kobayashi, 1921). In a series of papers on the endoparasitic worms from Japan, Kobayashi (1915b, 1915c, 1915d) reported anatomical features of the species (as *L. eurytremum*) using adult specimens from *S. asotus* and *T. nudiceps*. The same scientific name of the parasite was also used by Odhner (1927) for the Japanese specimens provided by Kobayashi. Subsequently, the species was reported as *Isoparorchis trisimiltubis* Southwell, 1913 (Yamaguti, 1934, 1938; Yamashita & Nishida, 1955; Uehara, 1972), but both *L. eurytremum* and *I. trisimiltubis* have been regarded as a junior synonym of *I. hypselobagri* in Japan (see Shimazu, 1999, 2002; Shimazu *et al.*, 2011). Recently, Shimazu *et al.* (2011) redescribed the species based on specimens from fishes in the Lake Biwa basin, central Honshu, Japan, and made a detailed historical review of the synonymy of the species. No molecular work using materials from Japan and other countries has so far been conducted.

Geographical distribution

The species has been found in the following 18 prefectures in Japan (Table 1): Gunma, Ibaraki, Chiba, Tokyo, Nagano, Shiga, Kyoto, Nara, Okayama, Shimane, Hiroshima, Yamaguchi, Ehime, Kochi, Fukuoka, Oita, Miyazaki, and Kumamoto. These prefectures are located in central and western Honshu, Shikoku, and Kyushu islands, all of which belong to the temperate portion of Japan. So far, the species has not been reported from the subarctic (e.g., northern Honshu and Hokkaido) and subtropical (e.g., Okinawa) portions of Japan.

Fish hosts

The species parasitizes various freshwater fishes in Japan. Based on the previous and present studies, 24 nominal and 2 unnamed species in 10 families

and 5 orders are known as its hosts (Table 1), which indicates that the host specificity of the parasite is not strict for fishes. Kobayashi (1915a) used “gigi” as the Japanese name for *P. aurantiacus*, but these names were a problematic use, because *P. aurantiacus* indicates a different species of bagrid called “gibachi” in Japanese. Thus, Kifune (1978) suggested the fish reported as “gigi” by Kobayashi (1915a) might have been “*Pelteobagrus nudiceps*.” Shimazu *et al.* (2011) also made a similar suggestion. As no Kobayashi’s (1915a) specimen of “gigi” or *P. aurantiacus* remains, it is impossible at present to clarify what species was examined by him. Therefore, following the original Japanese name of the fish, we adopt “gigi” and its most current scientific name, *T. nudiceps*, is used in this paper instead of *P. aurantiacus*. Okabe (1940) collected “*Isoparorchis* sp.” from an unspecified host but, according to Kifune (1978), it was *I. hypselobagri* from *Opsariichthys platypus* (as *Zacco platypus*). Also, Iwata *et al.* (2007) reported “*Isoparorchis* sp.” from *S. asotus*, and their specimens are herein regarded as *I. hypselobagri* based on the pictures (figs. 1–2 in Iwata *et al.*, 2007). On the other hand, Shimazu (2007) found a specimen of *Isoparorchis* from *Tandanus tandanus* in Satyu Yamaguti’s Collection deposited at the Meguro Parasitological Museum, Tokyo, but this host record is not included in Table 1, because he suggests that the specimen was collected in Australia.

Prevalence and intensity of infection

Infection levels of *I. hypselobagri* vary between fish species, fish sizes, or sampling localities. For example, 70.0% of 10 *Channa argus* (as *Ophicephalus argus*) from Lake Shinji, Shimane Prefecture, were infected with a mean intensity of 3.1 worms (intensity range: 0–5) (Yamashita & Nishida, 1955), while only 3.2% of 2,061 *Candidia temminckii* (as *Zacco temminckii*) from the Shirazuna River, Nara Prefecture, harbored up to 3 worms (mean intensity: 1.1 worms) (Sawada & Osako, 1969). In the latter fish sample, no worm was found in small fish (≤ 44 mm BL) but prevalence of infection steadily increased with an increase in fish size: 2.3, 8.1, and 14.5% for fish

of 45–70, 71–110, and ≥ 111 mm BL, respectively (Sawada & Osako, 1969).

Prevalence of infection by *I. hypselobagri* fluctuated seasonally in *C. temminckii* from the Shirazuna River (Sawada & Osako, 1969). Although it was high in late winter and spring (February to May), it decreased in early and mid-summer (June and July) and reached the lowest value in late summer (August). It, however, increased in fall (September to November) and showed high values in early and mid-winter (December and January). For the observed high prevalence in winter, Sawada & Osako (1969) suggested that cercariae of this parasite may invade the fish in fall after they develop in and emerge from snail intermediate hosts during summer, but since the parasite is known to use three hosts (i.e., snail first intermediate hosts, arthropod second intermediate hosts, and fish final hosts) to complete its life cycle (Besprozvannykh & Ermolenko, 1989), it may be reasonable to consider that *C. temminckii* gets infected by feeding on the second intermediate hosts in fall. On the other hand, Sawada & Osako (1969) gave no explanation for the decline in prevalence in summer, but it is likely that this summer decline in prevalence was caused by mortality of infected hosts after their spawning, because *C. temminckii* spawns in May to August and reduces its adult density in the population during summer and fall (Katano, 1989).

Distribution and maturation in fish

When worms parasitize the body muscles of *C. temminckii*, they occur in the tunnel-like tubes built by themselves (Sawada & Osako, 1969). The coloration of the tissues surrounding the tubes changes to blackish brown, and the skin near the infection site is swollen (see fig. 1 in Sawada & Osako, 1969). Similar tube formation and blackish pigmentation also have been reported from other Japanese fishes, such as *C. argus* (Yamashita & Nishida, 1955), *Hemibarbus barbus* (Kamegai *et al.*, 1972), and *Pungtungia herzi* (Kifune, 1978). It is not yet known how much the parasite affects the physiology and behavior of those infected fishes in Japan.

Mature worms (with eggs in the uterus) are found

in the air bladder of *S. asotus* (Kobayashi, 1915a, 1921; Yamaguti, 1934; Sawada & Osako, 1969; Shimazu, 2007; Iwata *et al.*, 2007; Shimazu *et al.*, 2011; this paper) but also occur in various body parts of some other fishes, i.e., the body cavity of *Silurus biwaensis* (Shimazu *et al.*, 2011), the air bladder of *T. nudiceps* (Kobayashi, 1915a, 1921), the body muscles of *C. temminckii* (Sawada & Osako, 1969; Kugi & Shiote, 1979; this paper), *O. platypus* (Kugi & Shiote, 1979), *Lepomis macrochirus* (Shimazu *et al.*, 2011) and *Micropterus salmoides* (Shimazu *et al.*, 2011), the hypodermal tissues and body muscles of *P. herzi* (Kifune, 1978: this paper), and around the air bladder and in the body cavity of *C. argus* (Suzuki *et al.*, 1967; Shimazu *et al.*, 2011). Mature worms from the air bladder of *S. asotus* were constantly large (up to 45.2 mm BL, see below), which suggests that this fish and the air bladder are quite suitable for the parasite as its final host and infection site.

Immature worms (with no eggs in the uterus) also occur in various body parts of various fish species: the body cavity of *S. asotus*, *Odontobutis obscura* (as *Mogruna obscura*), *C. temminckii*, *Gnathopogon elongatus elongatus*, *H. barbus*, *O. platypus*, *Acanthogobius flavimanus*, *Gymogobius urotaenia* (as *Chaenogobius macrognathus*), and *C. argus* (Kobayashi, 1915a, 1921; Yamaguti, 1934, 1938; Okabe, 1940; Yamashita & Nishida, 1955; Sawada & Osako, 1969; Kamegai *et al.*, 1972; this paper), hypodermal (as subcutaneous) tissues of *Tribolodon hakonensis* (as *Leuciscus hakonensis*) and *Sarcocheilichthys variegatus microoculus* (as *S. variegatus*) (Yamaguti, 1934), body muscles and flesh of *T. hakonensis*, *S. variegatus microoculus*, *H. barbus* and *C. argus* (Yamaguti, 1934; Yamashita & Nishida, 1955; Suzuki *et al.*, 1967; Kamegai *et al.*, 1972), air bladder and air bladder wall of *Anguilla japonica* and *O. obscura* (Yamaguti, 1934; this study), gut of *Rhinogobius* sp. BW (Shimazu *et al.*, 2011), stomach wall of *A. japonica* and *Cottus reini* (Shimazu *et al.*, 2011; this paper), intestine of *S. asotus* (Shimazu *et al.*, 2011), intestinal wall of *C. argus* (Suzuki *et al.*, 1967), liver and liver wall of *C. reini*, *R. fluvialis*, *Rhinogobius* sp. and *C. argus* (Yamashita &

Nishida, 1955; Suzuki *et al.*, 1967; Shimazu *et al.*, 2011; this paper), mesentery of *A. japonica*, *C. temminckii* and *P. herzi* (this paper), gonad wall of *C. argus* (Suzuki *et al.*, 1967), and gills of *T. nudiceps* (Kobayashi, 1915a, 1921). It is interesting to note that the percentage of occurrence of mature worms differs between body parts in the same host species: in *C. temminckii*, about 50% of the worms from the body muscles were mature, while the worms from the body cavity were all immature (Sawada & Osako, 1969).

Worms of various sizes are found in fish hosts. Mature and immature worms from *S. asotus* measured 20–40 mm BL and 8 mm BL, respectively (Shimazu *et al.*, 2011). A similarly large mature specimen (45.2 mm BL) was also collected from *S. asotus* in this study. However, mature worms from other fish species do not reach such a large size (e.g., 7.8–9.3 mm BL and 26.1 mm BL from *P. herzi* [Kifune, 1978; this study]; 9.6 mm BL from *C. temminckii* [this study]; 11 mm BL from *C. temminckii* or *O. platypus* [Kugi & Shiote, 1979]), suggesting that, even if those fishes harbor mature worms, they are less suitable for the parasite than *S. asotus*. Sawada & Osako (1969) reported a close positive relationship between body sizes of worms and their hosts (*C. temminckii*): larger worms occurred in larger fish, which implies that the worms have no short-life and grow with fish growth and age.

Life cycle

The life cycle of *I. hypselobagri* is poorly known in Japan. Kobayashi (1915a, 1922) suggested that the cercaria infecting freshwater snails *Semisulcospira libertina* (as *Melania libertina*) was identifiable as the species, but his suggestion was denied by Shimazu (1999, 2003). According to Shimazu (1999, 2003) and Shimazu *et al.* (2011), the morphology of *Cercaria introverta* Faust, 1924 from *Semisulcospira* spp. in Japan (Ito, 1964; Urabe, 2003) is similar to that of the cercaria of *I. hypselobagri* which was described in the Russian Far East (Besprozvannykh & Ermolenko, 1989). On the other hand, we consider that wild fishes become infected with the parasite in

two pathways through prey-predator relationships: one is feeding by fish final hosts on arthropod second intermediate hosts and the other is predation by large piscivorous fishes on small fishes. In these pathways, metacercariae and immature worms may be transferred, respectively, from the second intermediate hosts to the final hosts and from the prey fishes to the predators. Yamaguti (1934) experimentally succeeded in transferring immature worms (as larvae) from *O. obscura* to *S. asotus* and regarded *O. obscura* as a reservoir host. The previous works in Japan on *I. hypselobagri* focused on its morphology and occurrence in freshwater fishes, and our knowledge on the life cycle of the species is still limited: nothing is known, for example, about its second intermediate hosts in Japan. We need more work on various aspects of the life cycle of the parasite.

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