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REVIEW

A Checklist of the Parasites of Ayu (*Plecoglossus altivelis altivelis*) (Salmoniformes: Plecoglossidae) in Japan (1912–2007)

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Abstract The ayu or sweetfish *Plecoglossus altivelis altivelis* is distributed in many rivers and some lakes in Japan and also occurs in rivers of the Korean Peninsula and along the east coast of China and northern Vietnam. In Japan, this species is one of the most important freshwater fishes for commercial fisheries, aquaculture, and recreational fishing. In the present paper, information on the protistan and metazoan parasites of ayu in Japan is compiled based on the literature published for 96 years between 1912 and 2007, and the parasites, including 29 named species and those not identified to species level, are listed by higher taxon as follows: Ciliophora (no named species), Microspora (1), Myxozoa (1), Trematoda (13), Monogenea (3), Cestoda (1), Nematoda (1), Acanthocephala (3), Copepoda (4), and Branchiura (2). For each taxon of parasite, the following information is given: its currently recognized scientific name, any original combination, synonym(s), or other previous identification used for the parasite occurring in ayu; habitat (freshwater, brackish, or marine); site(s) of infection within or on the host; known geographical distribution in Japanese waters; and the published source of each locality record. There has been no record of parasites from a subspecies of ayu, the ryukyu-ayu *Plecoglossus altivelis ryukyuensis*. The myxozoan *Mitraspora plecoglossi* Fujita is transferred to the genus *Hoferellus* (as *H. plecoglossi* n. comb.), *Acanthocephalus opsariichthydis* Yamaguti, 1935 is determined to be the nomenclaturally correct spelling and date of that acanthocephalan species, and synonymy of the acanthocephalan *Echinorhynchus oblitus* Golvan with *E. cotti* Yamaguti is formally accepted.

Key words: ayu; checklist; *Echinorhynchus oblitus*; *Hoferellus plecoglossi* n. com.; parasites; *Plecoglossus altivelis altivelis*

INTRODUCTION

The ayu *Plecoglossus altivelis altivelis* Temminck and Schlegel, also called sweetfish, is a fish of the order Salmoniformes that belongs to the family Plecoglossidae (Hosoya, 2002). In Japan, ayu are distributed in many rivers and some lakes from western Hokkaido to southern Kyushu. A landlocked population of ayu inhabits Lake Biwa, central Japan. Ayu also occur in rivers of the Korean Peninsula and along the east coast of China and northern Vietnam. A population of ayu that previously inhabited Taiwan has gone extinct. The ryukyu-ayu *Plecoglossus altivelis ryukyuensis* Nishida is a subspecies of ayu that currently occurs only in streams on the island of Amami-Oshima

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in southern Japan (Hosoya, 2002). This subspecies currently has been successfully reintroduced into streams and lakes on the island of Okinawa (Ikehara, 2004), where it had gone extinct around 1980. Ayu are one of the most important freshwater fishes for commercial fisheries, aquaculture, and recreational fishing in Japan.

Much work has been conducted on the parasites of ayu in Japan because of their importance in fisheries and human parasitology, but the only review of these parasites (Kobayashi, 1938) is long out of date. To provide a comprehensive update, information on the protistan and metazoan parasites of ayu in Japan is compiled anew here based on the literature published for 96 years between 1912 and 2007. In total, 29 named species of parasites are listed herein along with those parasites not identified to species level. As far as we know, there has been no record of parasites from ryukyu-ayu *P. altivelis ryukyuensis*.

In the present checklist, parasites are arranged by higher taxon in the following order: Ciliophora, Microspora, Myxozoa, Trematoda, Monogenea, Cestoda, Nematoda, Acanthocephala, Copepoda, and Branchiura. The format is almost the same as in the checklists of Margolis and Arthur (1979) and McDonald and Margolis (1995). Within each higher taxon, genera and species are listed alphabetically. For each taxon of parasite, the following information is provided:

1) The current **scientific name**, including author(s) and date(s), followed by any original combination, recognized synonym(s), or other identifications(s) that have been used in establishing records from ayu in Japan. No attempt has been made to evaluate the taxonomic validity of the published reports; however, a generic reassignment is formally affirmed for the myxozoan *Mitraspora plecoglossi* as an absolute necessity under the current classification of this group. In addition, Harada's (1935) view that the acanthocephalan *Acanthocephalus aculeatus* is a junior synonym of *A. echigoensis* in not accepted herein because his proposal seems to require reassessment based on abundant material. On the other hand, the synonymy suggested by Amin et al. (2007) of two nominal species of the acanthocephalan genus *Echinorhynchus* is formally adopted herein.

2) The **habitat** in which the parasite was acquired and normally completes its life cycle is given as FW for fresh waters, B for brackish waters, and M for marine waters.

3) The **Site(s) of infection** of the parasite in or on its host. If the site was not given in the original record, the likely site was determined from other records and is enclosed in square brackets.

4) The **Distribution** of the parasite is indicated by prefecture (boundaries shown in Fig. 1), in geographical order from northeast to southwest. For marine or brackish-water species, the name of the prefecture nearest the collection site is given.

5) The **Record(s).** The authors responsible for the records are listed in chronological order. If a parasite has been reported more than once, the references are numbered, but not when there has been only one record of the parasite. Each reference is followed by the locality or localities given in two parts, first the prefecture(s) and then the detailed collection locality or localities from which the parasite was reported. If no locality record was given, the geographical locality is shown by a dash (—). When all records are from the same prefecture, only the detailed collection locality or localities are listed.

6) Under **Remarks**, explanatory comments are given on systematics, nomenclature, useful references, and notes on specific items such as tentative parasite identifications in the original reports.

7) The **References** section includes works directly cited in the Parasite List; the **Supplementary References** are publications dealing with various aspects of parasites of Japanese ayu but not

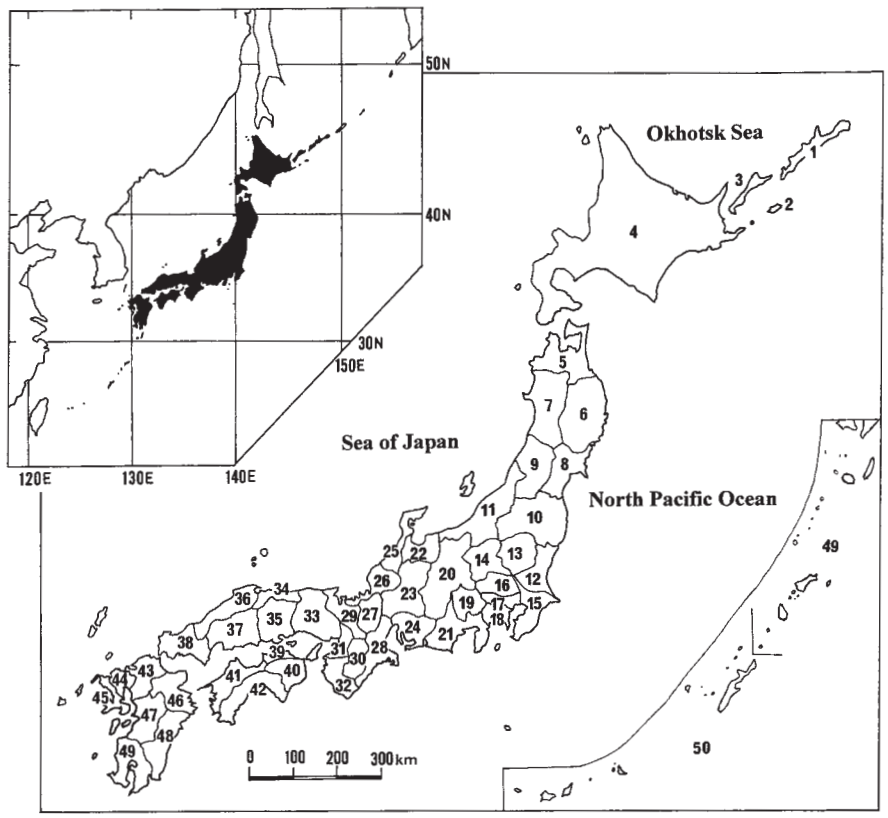

Fig. 1. Map of Japan showing the prefectural boundaries. The following prefectural names are arranged in alphabetical order: Aichi-24; Akita-7; Aomori-5; Chiba-15; Ehime-41; Etorofu Island-1; Fukui-26; Fukuoka-43; Fukushima-10; Gifu-23; Gunma-14; Hiroshima-37; Hokkaido-4; Hyogo-33; Ibaraki-12; Ishikawa-25; Iwate-6; Kagawa-39; Kagoshima-49; Kanagawa-18; Kochi-42; Kumamoto-47; Kunashiri Island-3; Kyoto-29; Mie-28; Miyagi-8; Miyazaki-48; Nagano-20; Nagasaki-45; Nara-30; Niigata-11; Oita-46; Okayama-35; Okinawa-50; Osaka-31; Saga-44; Saitama-16; Shiga-27; Shikotan Island-2; Shimane-36; Shizuoka-21; Tochigi-13; Tokushima-40; Tokyo-17; Tottori-34; Toyama-22; Wakayama-32; Yamagata-9; Yamaguchi-38; and Yamanashi-19.

containing original parasite records. If only a Japanese title was given by the original author(s), our translation of the title into English is provided in square brackets.

This checklist is the fifth in the following series of published synopses of the parasites of commercially important fishes and shellfishes in Japan: Nagasawa et al. (1987) for the parasites of salmonids; Nagasawa et al. (1989) for the parasites of freshwater fishes in Hokkaido; Nagasawa (1993a) for the parasites of squids and cuttlefishes; and Nagasawa (1993b) for the parasites of gadids.

PARASITE LIST

Ciliophora

Trichodina sp. (FW)

Site of infection: gills

Distribution: Aichi

Record: Nakajima et al. 1974 (Mito)

Remarks: There has been no study of the morphology and taxonomy of the species. The infected fish found in Aichi were transported as juveniles from Lake Biwa (Shiga) (Nakajima et al., 1974). The parasite was often found together with other gill parasites such as monogeneans *Dactylogyrus* sp. and copepods *Ergasilus* (as "*Pseudergasilus*") *zacconis* (Nakajima et al., 1974). Although there is a record of a similar parasite (as "*Cyclochaeta* sp.") from ayu in Taiwan (Abe, 1933; Kobayashi, 1938), Basson and Van As (1994) did not find any trichodinid infection of ayu from the Feitsui Reservoir in Taiwan.

MICROSPORA

Glugea plecoglossi Takahashi and Egusa, 1977 (FW)

Includes: *Glugea* sp. Awakura, 1974; Suzuki et al., 1974; Takahashi et al., 1975, 1979; Nakajima and Egusa, 1975a, 1975b, 1975c, 1979; Shiose and Tominaga, 1976; Inada and Hamaguchi, 1987

Sites of infection: visceral organs (pyloric caeca, abdominal cavity, abdominal membrane, ovary, testis, fat, spleen, liver, heart), musculature, gills, fins, eyes

Distribution: Kanagawa, Yamanashi, Nagano, Shiga, Okayama, Kochi, Miyazaki (see Remarks for possible further distribution)

Records: 1. Awakura 1974 (Okayama:—); 2. Suzuki et al. 1974 (Kanagawa: Freshwater Fish Propagation Experimental Station); 3. Takahashi et al. 1975 (Kanagawa: Freshwater Fish Propagation Experimental Station); 4. Nakajima and Egusa 1975a (Yamanashi: Fish Seedling Center); 5. Nakajima and Egusa 1975b (Yamanashi: Fish Seedling Center); 6. Nakajima and Egusa 1975c (Yamanashi: Fish Seedling Center); 7. Shiose and Tominaga 1976 (Nagano:—); 8. Takahashi and Egusa 1976 (Shiga:—); 9. Nakajima and Egusa 1976 (Yamanashi: Fish Seedling Center; Miyazaki: Prefectural Fisheries Experimental Station); 10. Takahashi and Egusa 1977a (Shiga: Prefectural Fisheries Experimental Station); 11. Takahashi and Egusa 1977b (Shiga: Prefectural Fisheries Experimental Station); 12. Takahashi and Egusa 1978 (Shiga:—); 13. Takahashi 1978 (Shiga: Lake Biwa); 14. Nakajima and Egusa 1979 (Shiga: Lake Biwa); 15. Takahashi et al. 1979 (Kanagawa: Freshwater Fish Propagation Experimental Station); 16. Dyková et al. 1980 (—); 17. Dyková and Lom 1980 (—); 18. Takahashi 1980 (Shiga: Lake Biwa); 19. Takahashi 1981 (Shiga: Lake Biwa): 20. Inada and Hamaguchi 1987 (Kochi: Freshwater Fisheries Laboratory); 21. Lom and Dyková 1992 (—); 22. Takahashi 1994 (Shiga:—); 23. Takahashi 1995 (Shiga:—); 24. Kim et al. 1996 (Shiga: Prefectural Fisheries Experimental Station); 25. Kamaishi et al. 1996a (Shiga: Lake Biwa [as "Lake Biwako"]); 26. Kamaishi et al. 1996b (Shiga: Lake Biwa [as "Biwako Lake"]); 27. Takahashi and Ogawa 1997 (Shiga: Prefectural Fisheries Experimental Station); 28. Kim et al. 1997 (Shiga: Prefectural Fisheries Experimental Station); 29. Kim et al. 1998 (Shiga: Prefectural Fisheries Experimental Station); 30. Kim et al. 1999 (Shiga: Prefectural Fisheries Experimental Station); 31. Lee et al. 2000 (Shiga: Prefectural Fisheries Experimental Station); 32. Lee et al. 2004 (Shiga: Prefectural Fisheries Experimental Station); 33. Lom and Dyková 2005 (—)

Remarks: Based on the results of questionnaire survey, Takahashi (1981) reported that infection of ayu by this parasite was found from 1968–1977 at fish farms in 12 prefectures (Gunma, Yamanashi, Nagano, Shizuoka, Aichi, Shiga, Mie, Okayama, Tokushima, Oita, Kumamoto,

Kagoshima), at seed production facilities in 11 prefectures (Kanagawa, Yamanashi, Nagano, Gifu, Fukui, Mie, Yamaguchi, Tokushima, Oita, Kumamoto, Miyazaki), and in natural waters in six prefectures (Gifu, Fukui, Okayama, Kochi, Kumamoto, Miyazaki). Egusa and Masuda (1971) also noted the occurrence of microsporan disease caused by the parasite (as "*Plistophora*" or "*Glugea*") in ayu at a fish farm in Oita. Although Grygier (2004) suggested that *G. plecoglossi* is endemic to Lake Biwa and its basin, the species has a wide distribution in Japan, but it is unknown whether its current distribution pattern has resulted from efforts of stocking ayu caught in the lake to many rivers. The species occurs in ayu cultured in Taiwan as well (Chu et al., 1990).

Myxozoa

Hoferellus plecoglossi (Fujita, 1927) n. comb. (FW)

Original combination: *Mitraspora plecoglossi* Fujita, 1927

Site of infection: kidney

Distribution: Shiga

Record: Fujita 1927 (Lake Biwa)

Remarks: The genus *Mitraspora* was long ago synonymized with the genus *Hoferellus* (Lom, 1963). Although 25 species are currently included in the latter genus (Lom and Dyková, 2006), the names of only three nominal species considered to be validly included in *Hoferellus* after transfer from *Mitraspora* have ever been mentioned explicitly. In their book, Lom and Dyková (1992) briefly summarized the biology of three such species, *H. cyprini* (the type species of *Mitraspora*), *H. carassii*, and *H. gilsoni*. Later, Lom and Dyková (2006) again provided information on *H. cyprini* and *H. carassii*. Thus, as far as we know, there has been no explicit proposal of generic transfer of the nominal species *M. plecoglossi*, and this species is herein formally transferred to *Hoferellus*.

Unidentified Myxozoa (FW)

Site of infection: unknown

Distribution: Gifu

Record: Anonymous 2002 (a tributary of the Kiso River)

Trematoda

Allocreadium sp. (FW)

Site of infection: intestine

Distribution: Shiga

Records: 1. Kataoka and Momma 1933b (Lake Biwa and streams emptying into the lake); 2. Kataoka and Momma 1934a (Lake Biwa and streams emptying into the lake)

Remarks: Kataoka and Momma (1933b, 1934a) reported that this species resembled *Dimerosaccus* (as "*Allocreadium*") *oncorhynchi*, but Shimazu (1988, 1999a, 2003) stated that it is not *D. oncorhynchi*.

Asymphylodora sp. (metacercaria) (FW)

Previous identification: *Asymphylodora tincae* of Date, 1943

Site of infection: unknown

Distribution: Okayama

Record: Date 1943 (Asahi River)

Remarks: Although some of the metacercariae found in ayu were identified by Date (1943) as *Asymphylodora tincae*, there was no morphological description. Yamaguti (1938) suggested that larval worms reported as *A. tincae* from Japan were a different species. The identification by Date (1943) needs confirmation and no specific name for this parasite is given herein. *Asymphylodora macrostoma* and *A. japonica* occur in Japan and the former species is known to infect fishes as metacercaria and adults (Shimazu, 1992, 1999a, 2003).

Clonorchis sinensis (Cobbold, 1875) (metacercaria) (FW)

Site of infection: fins

Distribution: Okayama

Record: Date 1943 (Asahi River)

Remarks: Date (1943: 1499–1500) reported metacercariae of this species from ayu but provided no detailed information on their morphology and taxonomy. The identification needs confirmation.

Echinochasmus japonicus Tanabe, 1926 (metacercaria) (FW)

Site of infection: gills

Distribution: Okayama

Records: 1. Tanabe 1926 (—); 2. Date 1943 (Asahi River)

Remarks: Information on this species is available from Komiya (1965).

Echinochasmus milvi Yamaguti, 1939 (metacercaria) (FW)

Site of infection: gills

Distribution: Fukuoka, Oita, Kagoshima

Record: Koga 1952a (Fukuoka: Yoshii; Oita: Hita; Kagoshima: Sendai River)

Remarks: Information on this species is available from Komiya (1965a, 1965b) as well as Koga (1952a).

Echinochasmus perfoliatus (Ratz, 1908) (metacercaria) (FW)

Site of infection: gills

Distribution: Okayama, Fukuoka

Records: 1. Okabe 1940 (Fukuoka: Ima River, Muromi River); 2. Date 1943 (Okayama: Asahi River)

Remarks: Information on this species is available from Komiya (1965a, 1965b).

Echinostomatidae gen. (FW)

Site of infection: unknown

Distribution: Gifu

Record: Anonymous 2002 (a tributary of the Kiso River)

Exorchis oviformis Kobayashi, 1915 (metacercaria) (FW)

Sites of infection: musculature, gills, fins

Distribution: Niigata, Shiga, Fukuoka

Records: 1. Okabe 1940 (Fukuoka: Naka River); 2. Sakai 1954 (Shiga: Lake Biwa); 3. Saito et al. 1964 (Niigata: Lake Yoroigata)

Remarks: Information on this species is available from Okabe (1940) and Komiya (1965a, 1965b).

Metagonimus miyatai Saito, Chai, Kim, Lee and Rim, 1987 (metacercaria) (FW)

Includes: *Metagonimus* sp. Miyata type of Saito, 1984

Sites of infection: scales, fins

Distribution: Yamagata, Miyagi, Shizuoka, Gifu, Hyogo, Hiroshima

Records: 1. Saito 1984 (Yamagata:—; Miyagi:—; Hiroshima: Ohta River); 2. Saito et al. 1997 (Yamagata: Oguni River; Miyagi: Natori River; Hiroshima: Ota River [as "Ohta River"]); 3. Kankawa and Uga 2001 (Hyogo: Chigusa River); 4. Anonymous 2002 (Gifu: a tributary of the Kiso River); 5. Kino et al. 2006 (Shizuoka: Kano River, Matsu River, Kawazu River, Inousawa River, Naka River, Warashina River, Asahina River, Ota River [as "Ohta River"], Tenryu River, Atago River, Miyakoda River, Kurumegi River, Iinoya River, Ai River, Ohchise River)

Remarks: Based on recent studies (Saito, 1984; Saito et al., 1997; Kankawa and Uga, 2001; Kino et al., 2006), it is clear that metacercariae of *Metagonimus miyatai* are commonly found in ayu in Japan. Although another species, *Metagonimus yokogawai*, has been recorded frequently from ayu (see the Records of the species given below), it is highly likely that the past records of *M. yokogawai* include *M. miyatai*. The life history of *M. miyatai* was reported by Shimazu (2002). This species is found in Korea as well (e.g., Saito et al., 1997). Information on the species is also available from Saito (1992, 1999, 2003, 2004).

Metagonimus takahashii Suzuki in Takahashi, 1929 (metacercaria) (FW)

Sites of infection: [scales]

Distribution: Gifu, Shimane

Records: 1. Takahashi 1967 (Shimane: Takatsu River); 2. Anonymous 2002 (Gifu: a tributary of the Kiso River)

Remarks: Takahashi (1967) obtained two species of adult worm, which were identifiable as *M. takahashii* and *M. yokogawai*, based on their egg sizes, by experimental infection of a dog by feeding it a single whole ayu from the Takatsu River. Saito (1973), however, experimentally showed that *M. takahashii* infects goldfish (*Carrasius carrasius auratus*) but not ayu. Thus, the identification by Takahashi (1967) requires confirmation. The identification by Anonymous (2002) was tentative.

Metagonimus yokogawai (Katsurada, 1912) Katsurada, 1912 (metacercaria) (FW)

Original combination: *Heterophyes yokogawai* Katsurada, 1912

Synonym: *Loxotrema ovatus* Kobayashi, 1912

Includes: *Metagonimus* spp. of Ito and Mochizuki, 1968

Digenean metacercariae of Kariya and Hamada, 1913; Egusa and Masuda, 1971

Sites of infection: musculature, scales, gills, opercula, fins, viscera

Distribution (Fig. 2): Hokkaido, Aomori, Iwate, Akita, Miyagi, Yamagata, Niigata, Ibaraki, Tochigi, Saitama, Tokyo, Kanagawa, Yamanashi, Nagano, Shizuoka, Toyama, Gifu, Aichi, Ishikawa, Fukui, Shiga, Kyoto, Osaka, Hyogo, Tottori, Okayama, Shimane, Hiroshima, Yamaguchi, Tokushima, Ehime, Kochi, Fukuoka, Saga, Nagasaki, Oita, Kumamoto, Miyazaki, Kagoshima

Records: 1. Katsurada 1912a (Okayama:—); 2. Katsurada 1912b (Okayama: Asahi River); 3. Katsurada 1912c (Gifu: Nagara River); 4. Kobayashi 1912 (Tokyo: Tama River; Shiga: Lake Biwa; Tokushima: Aga River, Yoshino River); 5. Katsurada 1912d (Gifu: Nagara River); 6. Kariya and Hamada 1913 (Osaka: Yodo River, Shinyodo River; Hyogo: Kako River; Tokushima: Yoshino River); 7. Usami 1914 (Gifu: Nagara River); 8. Muto 1917 (Shizuoka: Okitsu River); 9. Yamaguchi 1918 (Niigata: Hayade River, Miomote River, Aburuma River, Aga River); 10. Mukai 1919 (Kagoshima: Sendai River); 11. Koga (Kumamoto: Kuma River); 12. Takahashi 1929b (Gifu: Nagara River; Okayama: Asahi River); 13. Kishimoto 1932 (Osaka: Municipal Public Market); 14. Izumi 1935 (Hyogo: Muko River); 15. Taki 1935 (Oita: Okata River, Oita River, Banjo River, Mikuma River, Yamakuni River, Yakkan River); 16. Koga 1938 (Fukuoka: Yabe River; Oita: Chikugo River, Ono River, Yamakuni River, Oita River; Miyazaki: Gokase River, Mimitsu River; Kumamoto: Kuma River); 17. Koga 1939 (Oita: Chikugo River); 18. Marugame 1940 (Osaka: Yodo River); 19. Kokame 1941 (Hiroshima: Mitsu River); 20. Date 1943 (Okayama: Asahi River); 21. Watanabe and Horii 1950 (Shiga: Shiriuchi River); 22. Kubo 1950 (Osaka: Kanzaki River); 23. Takabayashi 1953 (Yamaguchi: Misumi River); 24. Morishita and Kobayashi (Aichi: Toyo River); 25. Sakai 1954 (Shiga: Lake Biwa); 26. Asada et al. 1957 (Hiroshima: Ashida River); 27. Ochi 1957 (Hyogo: Kanzaki River, Muko River, Kako River, Ibo River; Okayama: Takahashi River, Asahi River, Yoshii River; Hiroshima: Ashida River, Nuta River, Ota River, Gono River; Yamaguchi: Nishiki River, Saba River, Asa River); 28. Iwakura and Tanikawa 1957 (Miyazaki: Hitotsuse River, Sanzai River); 29. Iwakura and Tanikawa 1958 (Miyazaki: Kita River, Gokase River, Isuzu River, Mimi River, Omaru River, Hokita River, Sanzai River, Aya River, Kiyotake River, Kitago River, Sakatani River); 30. Sakai 1962 (Hyogo: Kako River; Okayama: Asahi River, Takahashi River; Tottori: Tenjin River; Shimane: Gono River, Takatsu River; Hiroshima: Ota River, Nuta River, Ashida River; Yamaguchi: Yoshida River, Saba River); 31. Kagei 1966 (Shimane: Takatsu River); 32. Oshima et al. 1966 (Shimane: Takatsu River); 33. Takahashi 1967 (Shimane: Kando River, Takatsu River; Oita: Chikugo River); 34. Ito et al. 1967 (Shizuoka: Kano River, Okitsu River, Abe River, Ooi River, Tenryu River, Miyakoda River, fish farms in Mori and Matsutomi); 35. Kagei and Oshima 1968 (Hokkaido: Furubira River; Iwate: Hei River, Sakari River, Kesen River; Akita: Hinokinai River; Miyagi: Eai River; Niigata: Tsubaki River, Uono River, Hayade River, Agano River; Ibaraki: Naka River; Tochigi: Omoi River, Kinu River, Naka River; Saitama: Ara River, Otsupe River; Kanagawa: Sagami River; Yamanashi: Fuefuki River; Nagano: Chikuma River; Gifu: Miya River, Ibi River; Fukui: Asuwa River; Kyoto: Yura River; Hyogo: Ibo River, Chigusa River; Okayama: Yoshii River, Asahi River; Shimane: Gono River, Takatsu River; Hiroshima: Nuta River, Kamo River; Yamaguchi: Nishiki River, Shimada River; Ehime: Shigenobu River, Hiji River, Shimanto River, Osu River; Kochi: Kagami River, Yoshino River, Monobe River, Yasuda River; Saga: Tamashima River; Nagasaki: Shisa River; Oita: Hita River; Kumamoto: Kuma River; Miyazaki: Gokase River, Isuzu River, Omaru River, Hitotsuse River, Sanzai River, Aya River, Kitago River; Kagoshima: Beppu River, Amori River, Gotanda River); 36. Saito 1968a (Yamagata: Aka River; Niigata: Miomote River, Ara River, Oishi River, Agano

River, Uono River; Toyama: Sho River; Ishikawa: Omi River; Shimane: Takatsu River); 37. Saito 1968b (Niigata: Uono River; Shimane: Takatsu River); 38. Okabe et al. 1968 (Oita: Chikugo River); 39. Komiya and Enomoto 1968 (—); 40. Ito and Mochizuki 1968 (Shizuoka:—); 41. Yokogawa and Sano 1968 (Ehime: Hiji River); 42. Kagei and Kihata 1970 (Shimane: Takatsu River); 43. Egusa and Masuda 1971 (Oita: fish farm in Yufuin); 44. Gyoten et al. 1971 (Ehime: Hiji River); 45. Yoshimura et al. 1972 (Akita: Chōkai); 46. Nakade 1972 (Aomori: Iwaki River; Akita: Yoneshiro River, Omono River, Koyoshi River); 47. Kobayashi 1972 (Shizuoka: Kano River); 48. Kobayashi et al. 1972 (Shizuoka: Kano River); 49. Saito 1972 (—); 50. Gyoten et al. 1972 (Ehime: Hiji River); 51. Saito 1973 (—); 52. Kagei and Kihata 1973 (Akita: Zinego River; Tochigi: Kasuo River; Ibaraki: Kuji River; Saitama: Otsupe River; Shizuoka: Kano River; Ishikawa: Otsuki River; Gifu: Nagara River; Shimane: Takatsu River; Hiroshima: Nuta River [as "Numata River"]; Yamaguchi: Shimada River, Nishiki River; Ehime: Hiji River; Kochi: Shimanto River; Nagasaki: Shisa River; Saga: Tamashima River; Kagoshima: Beppu River [as "Betsupu River"]); 53. Gyoten et al. 1973 (Ehime: Hiji River); 54. Kagei et al. 1974 (Tokyo: Central Wholesale Market; Shizuoka: Numazu Bay; Shiga: Lake Biwa; Wakayama:—; Kagoshima:—); 55. Tani et al. 1974 (Akita: Ani River, Babame River, Asahi River, Koyoshi River, Noshiro); 56. Akahane et al. 1980 (Shiga: Lake Biwa); 57. Akahane et al. 1983 (Shiga: Lake Biwa, fish farms in Kutsuki and Adogawa); 58. Saito 1984 (Miyagi:—; Hiroshima: Ota River; Fukuoka:—); 59. Saito et al. 1984 (Yamagata: Arase River,

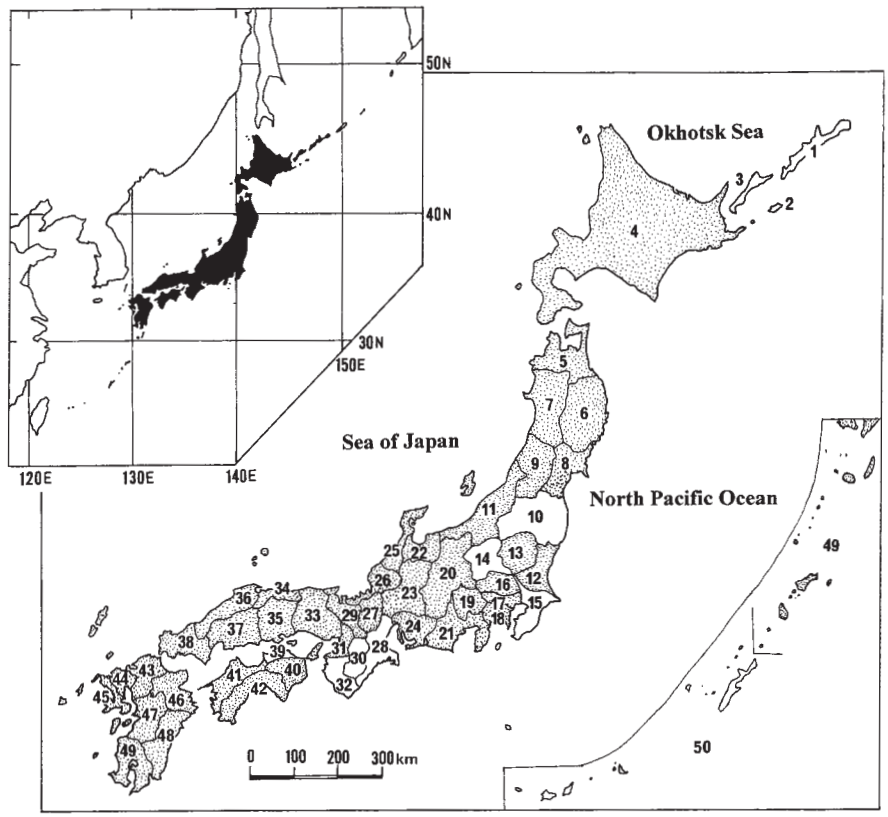

Fig. 2. Map of Japan showing the prefectures where the metacercariae of *Metagonimus yokogawai* occurred in ayu (stippled). See Fig. 1 for the prefectural names.

Sake River, Oguni River, Nyu River, Mogami River, Mamigasaki River, Haguro River, Nezugaseki River, Atsumi River; Miyagi:—; Hiroshima:—; Fukuoka:—); 60. Fujino et al. 1989 (Hiroshima: Ota River); 61. Ito et al. 1991 (Shizuoka: Atago River, Ohchise River, Ai River, Kurumegi River, Miyakoda River); 62. Yoshida et al. 1991 (Wakayama:—); 63. Saito et al. 1997 (Miyagi: Natori River; Hiroshima: Ota River [as "Ohta River"]); 64. Uchida et al. 1999 (Shizuoka: Haya River, Fujiki River, Sakawa River, Kano River, Raikou River, fish farms along the Kano River); 65. Kankawa and Uga 2001 (Hyogo: Chigusa River); 66. Kino et al. 2006 (Shizuoka: Kano River, Matsu River, Kawazu River, Inousawa River, Naka River, Okitsu River, Asahina River, Ooi River, Ota River [as "Ohta River"], Miyakoda River, Kurumegi River, Aika River, Ohchise River)

Remarks: Since *Metagonimus yokogawai* is one of the most important fish parasites infecting humans in East Asia, many studies on the species have been conducted in Japan from medical and epidemiological viewpoints. However, not all the records of *M. yokogawai* listed herein are likely to concern this species; records of a very closely related species, *M. miyatai* (above), must be mixed in because strict differentiation of the two species could not be done before the description of the latter species by Saito et al. (1987) and really did not begin until Saito et al. (1997). Concurrent infection by both parasites is also common in ayu (Kino et al., 2006). It will be necessary in future studies to strictly identify the species by examining adult worms obtained from experimental mammalian hosts and to reevaluate the previously recorded geographical distributions of both species in Japan. There is a difference in preferred site of infection between two species: *M. yokogawai* prefers the musculature, but *M. miyatai*, the scales (Saito, 1984; Kino et al., 2006). Although Saito (1984) did not mention which type of *Metagonimus* metacercariae he recovered from ayu in Fukuoka, the record is included here under *M. yokogawai* because the site of infection was mainly the musculature. Detailed information on the taxonomy, life history, and ecology of *M. yokogawai* in Japan is available from Ito (1963, 1964) although the two species were not clearly differentiated in these works.

Metorchis orientalis Tanabe, 1920 (metacercaria) (FW)

Site of infection: under skin

Distribution: Osaka

Record: Kubo 1950 (Kanzaki River)

Remarks: Information on this species is available from Komiya (1965a, 1965b).

Microparyphium kyushuensis Koga, 1952 (metacercaria) (FW)

Site of infection: gills

Distribution: Kagoshima

Record: Koga 1952b (Sendai River)

Remarks: Information on this species available from Komiya (1965a, 1965b) as well as Koga (1952b).

Nanophyetus japonenis Saito, Saito, Yamashita, Watanabe and Sekikawa, 1982 (metacercaria) (FW)

Sites of infection: kidney, musculature

Distribution: Yamagata, Niigata

Record: Saito et al. 1982 (—)

Remarks: The larval stage of this species was described by Saito (1985).

Neoplagioporus ayu (Takahashi, 1928) Shimazu, 1990 (FW)

Original combination: *Podocotyle ayu* Takahashi, 1928

Site of infection: intestine

Distribution: Kyoto, Okayama

Records: 1. Takahashi 1928 (Okayama: Asahi River); 2. Takahashi 1929a (—); 3. Yamaguti 1934a (—); 4. Shimazu 1990a (Kyoto: Hozu River, Yura River)

Remarks: According to Shimazu (1990a), the collection localities of Yamaguti's (1934a) specimens were the Hozu River and the Yura River.

Pseudexorchis major (Hasegawa, 1935) Yamaguti, 1938 (metacercaria) (FW)

Original combination: *Exorchis major* Hasegawa, 1935

Sites of infection: scales, fins, gills, opercula, mouth cavity wall, musculature

Distribution: Shiga, Osaka, Okayama, Hiroshima, Fukuoka

Records: 1. Hasegawa 1934 (Okayama: Seno); 2. Hasegawa 1935 (Okayama:—); 3. Okabe 1940 (Fukuoka: Muromi River); 4. Marugame 1940 (Osaka: Yodo River); 5. Kokame 1941 (Hiroshima: Mitsu River); 6. Date 1943 (Okayama: Asahi River); 6. Sakai 1954 (Shiga: Lake Biwa)

Remarks: Information on this species is available from Komiya (1965a, 1965b).

Unidentified Trematoda (metacercaria) (FW or B/M)

Site of infection: skin, scales, fins, gills, body cavity

Distribution: Akita, Gifu, Nara

Records: 1. Usami 1915 (Gifu: Nagara River); 2. Imagawa 1934 (Akita: coastal waters of Lake Hachirogata); 3. Nakamura et al. 2000 (Nara: Takami River)

Monogenea

Dactylogyrus sp. (FW)

Site of infection: gills

Distribution: Aichi, Hiroshima

Records: 1. Kondo 1969 (Hiroshima: Shobara); 2. Nakajima et al. 1974 (Aichi: Mito)

Remarks: There was no morphological and taxonomical study of this species and thus the identification needs to be confirmed. In one instance, the fish infected by the species were transported as juveniles from Lake Biwa (Shiga) to Aichi (Nakajima et al., 1974).

Gyrodactylus japonicus Kikuchi, 1929 (FW)

Site of infection: fins

Distribution: Nagano, Tokushima, Fukuoka

Records: 1. Kikuchi 1929 (—); 2. Ogawa and Egusa 1978 (Nagano:—; Tokushima:—); 3. Inada et al. 1990 (Fukuoka:—)

Remarks: Ogawa and Egusa (1978) suggested that three species of *Gyrodactylus* (*G. japonicus, G. plecoglossi, G. tominagai*) found in Nagano and Tokushima were of Lake Biwa origin (Shiga)

because the host fish had been transported from the lake.

Gyrodactylus plecoglossi Ogawa and Egusa, 1978 (FW)
Site of infection: fins
Distribution: Nagano, Tokushima
Record: Ogawa and Egusa 1978 (Nagano:—; Tokushima:—)
Remarks: See Remarks on *G. japonicus*.

Gyrodactylus tominagai Ogawa and Egusa, 1978 (FW)
Site of infection: fins
Distribution: Nagano, Tokushima
Record: Ogawa and Egusa 1978 (Nagano:—; Tokushima:—)
Remarks: See Remarks on *G. japonicus*.

Gyrodactylus spp. (FW)
Sites of infection: fins, gills
Distribution: Shiga, Nara
Records: 1. Nakamura et al. 2000 (Nara: Takami River); 2. Ninomiya and Yamamoto 2004 (Prefectural Fisheries Experimental Station); 3. Suzuki 2006 (—)

CESTODA

Proteocephalus plecoglossi Yamaguti, 1934 (FW)
Previous identification: *Proteocephalus neglectus* of Kataoka, 1932; Kataoka and Momma, 1933a, 1933b; Momma, 1935
Includes: *Proteocephalus* sp. of Kataoka, 1930, 1932; Inoue, 1932
Sites of infection: intestine, stomach, pyloric caeca
Distribution: Shiga, Hyogo
Records: 1. Kataoka 1930 (Shiga: Lake Biwa, Ado River, Ishida River, Amano River; Hyogo: Ina River); 2. Inoue 1932 (Shiga: Ado River, Shiriuchi River); 3. Kataoka 1932 (Shiga: Lake Biwa); 4. Kataoka and Momma 1932a (Shiga: Lake Biwa); 5. Kataoka and Momma 1933a (Shiga: Lake Biwa and streams emptying into the lake); 6. Kataoka and Momma 1933b (Shiga: Lake Biwa and streams emptying into the lake); 7. Kataoka and Momma 1934a (Shiga: Lake Biwa and streams emptying into the lake); 8. Yamaguti 1934b (Shiga: Lake Biwa); 9. Momma 1935 (Shiga: Lake Biwa); 10. Takahashi 1973 (Shiga: Lake Biwa, Echi River, Ane River, Ishida River, Shiriuchi River, Yasu River); 11. Shimazu 1990b (Shiga: Lake Biwa); 12. Shimazu 1993 (Shiga: Lake Biwa); 13. Hypša et al. 2005 (Shiga: Lake Biwa); 14. Scholz et al. 2007 (Shiga: Lake Biwa)
Remarks: This species is endemic to Lake Biwa and its basin (Grygier, 2004). The fish infected by this parasite from the Ina River (Hyogo) (Kataoka, 1930) were transplanted from Lake Biwa (Shiga) (see Kataoka and Momma, 1932a, footnote of table). The cyclopoid copepod *Eucyclops* (as "*Cyclops*") *serrulatus* is an experimental intermediate host of this parasite (Kataoka and Momma, 1934b). Iwata (1938) discussed the scientific name of *P. plecoglossi*. Nagasawa et al. (2007) suggested that the species might be used from spring to summer as a biological tag to identify

ayu of Lake Biwa origin stocked into rivers in Japan. Information on *P. plecoglossi* is available from Shimazu (1997).

Nematoda

Raphidascaris gigi Fujita, 1928 (larva and adult) (FW)

Synonyms: *Raphidascaris biwakoensis* Fujita, 1928; *Raphidascaris plecoglossi* Fujita, 1928

Sites of infection: abdominal cavity (larva), stomach, intestine (adult)

Distribution: Hokkaido, Shiga

Records: 1. Fujita 1928 (Shiga: Lake Biwa); 2. Kataoka and Momma 1933b (Shiga: Lake Biwa and streams emptying into the lake); 3. Kataoka and Momma 1934a (Shiga: Lake Biwa and streams emptying into the lake); 4. Awakura 1968 (Hokkaido: unspecified locality); 5. Satoi 1994 (Shiga: Lake Biwa); 6. Satoi and Tsumura 1994 (Shiga: Lake Biwa); 7. Satoi 1995 (Shiga: Lake Biwa); 8. Satoi 1996 (Shiga: Lake Biwa)

Remarks: This species is endemic to Lake Biwa and its basin (Grygier, 2004). Awakura (1968) found this nematode in ayu cultured in Hokkaido but the fish he examined had been transported from Lake Biwa (Shiga). A planktonic intermediate host of the nematode is the cladoceran *Leptodora kindti* (Kataoka and Momma, 1932b; Moravec et al., 1998). The ayu serves as the definitive host (adult worms free in the digestive tract) as well as an intermediate or paratenic host (larvae encapsulated in the abdominal cavity) (Fujita, 1928; Kataoka and Momma, 1934a). Moravec and Nagasawa (2002) discussed the nomenclature of three species of *Raphidascaris* (*R. gigi, R. biwakoensis, R. plecoglossi*) described by Fujita (1928) from Lake Biwa and concluded that *R. gigi* is the valid name, Yamaguti (1935b) having acted as first reviser to establish its priority. Fujita (1928) erroneously reported the site of infection of larvae of the species as the "intestine" (for *R. biwakoensis*) or "pleural cavity" (for *R. plecoglossi*) in the English abstract, but it was actually the abdominal cavity, as written in the Japanese text. Nagasawa et al. (2007) suggested that this species should be more useful than the cestode *Proteocephalus plecoglossi* a biological tag to identify ayu of Lake Biwa origin stocked into rivers in Japan. Information on *R. gigi* is available from Shimazu (1998).

Acanthocephala

Acanthocephalus aculeatus Van Cleave, 1931 (FW)

Site of infection: intestine

Distribution: Shiga

Records: 1. Kataoka and Momma 1933b (Lake Biwa and streams emptying into the lake); 2. Kataoka and Momma 1934a (Lake Biwa and streams emptying into the lake)

Remarks: This species was reduced by Harada (1935) to a junior synonym of *Acanthocephalus echigoensis*, but the scientific name reported by Kataoka and Momma (1933b, 1934a) is given herein because Harada's view seems to need reassessment based on abundant material. In his review, Kobayashi (1938) reported this species as *A. echigoensis*. Kataoka and Momma (1933b) provided two microphotographs of the species (a male and a female) and described it in Japanese. In a recent survey of Lake Biwa area fish acanthocephalans, in which mostly very

young ayu were examined (Amin et al., 2007), *A. aculeatus* was not encountered.

Acanthocephalus opsariichthydis Yamaguti, 1935 (FW)

Site of infection: intestine

Distribution: Nagano

Record: Yamaguti 1939a (Lake Suwa)

Remarks: This species was initially described as *A. opsalichthydis* by Yamaguti (1935a). However, since the true spelling of the host genus was *Opsariichthys*, which he misspelled *Opsalichthys* in 1935, Yamaguti (1939a) proposed the change of the species name to *opsariichthydis*. This proposal would ordinarily be an unjustified emendation under International Code of Zoological Nomenclature Article 33.2, due to the lack of any vidence of a *lapsus* within the 1935 work itself (International Commission on Zoological Nomenclature, 1999). Nonetheless, since Yamaguti's (1939a) proposal, the species has been reported as "*Acanthocephalus opsariichthydis* Yamaguti, 1935" (not *A. opsalichthydis* Yamaguti, 1935 nor *A. opsariichthydis* Yamaguti, 1939) in all 10 papers and monographs that have dealt with it worldwide (Petrochenko, 1956; Yamaguti, 1963; Ichihara, 1964; Golvan, 1969; Nakajima et al., 1975; Nakajima and Egusa, 1975d; Nagasawa et al., 1983; Amin, 1985; Shimazu, 1999; Amin et al., 2007). The emended spelling has thus without any question come to enjoy "prevailing usage", with general attribution to the original author. Under Article 33.2.3.1, *opsariichthydis* has therefore become a justified emendation and the valid name of the species, and it takes the 1935 date.

Echinorhynchus cotti Yamaguti, 1935 (FW)

Synonym: *Echinorhynchus oblitus* Golvan, 1969

Includes: *Echinorhynchus* sp. of Kakaoka and Momma, 1933b, 1934a

Site of infection: intestine

Distribution: Shiga

Records: 1. Kataoka and Momma 1933b (Lake Biwa and streams emptying into the lake); 2. Kataoka and Momma 1934a (Lake Biwa and streams emptying into the lake); 3. Amin et al. 2007 (Lake Biwa)

Remarks: The acanthocephalan reported by Kataoka and Momma (1934a) as *Echinorhynchus* sp. was described by Golvan (1969) as a new species, *E. oblitus*. In his classification of Acanthocephala, Amin (1985) listed *E. oblitus* as a valid species; however, Amin et al. (2007) recently stated that Kataoka and Momma's species is likely *E. cotti* and that *E. oblitus* is an invalid species. We here take the step of formally adopting this synonymy. Kataoka and Momma (1933b) provided two microphotographs, one of which showed its partly retracted proboscis.

COPEPODA

Ergasilus plecoglossi Yamaguti, 1939 (FW)

Site of infection: gills

Distribution: Okayama

Record: Yamaguti 1939b (Kakogawa)

Remarks: There has been no record of this species since its original description by Yamaguti (1939b).

Ergasilus zacconis (Yamaguti, 1936) Kim and Choi, 2003 (FW)

Original combination: *Pseudergasilus zacconis* Yamaguti, 1936

Includes: *Ergasilus* sp. of Kondo 1969

Site of infection: gills

Distribution: Aichi, Okayama, Hiroshima

Records: 1. Kondo 1969 (Hiroshima: Shobara); 2. Nakajima and Egusa 1973 (Okayama: Seto); 3. Nakajima et al. 1974 (Aichi: Mito)

Remarks: This species was initially placed in the genus *Pseudergasilus* by Yamaguti (1936); this, however, has been regarded recently as a junior synonym of *Ergasilus* by Kim and Choi (2003). Also, *Pseudergasilus* was not listed as a valid genus in the monographs by Gusev (1987) and Boxshall and Halsey (2004). The species was originally described by Yamaguti (1936) from the pale chub *Zacco platypus* (Cyprinidae) in Lake Suwa, central Japan, and was recently redescribed by Kim and Nagasawa (2006) from the same host species in Hiroshima. Ayu infected by *E. zacconis* found in Aichi and Okayama were transported as juveniles from Lake Biwa (Shiga) (Nakajima and Egusa, 1973; Nakajima et al., 1974).

Lernaea cyprinacea Linnaeus, 1758 (FW)

Synonym: *Lernaea elegans* Leigh-Sharpe, 1915

Site of infection: [head embedded in musculature with body protruding externally]

Distribution: unknown

Records: 1. Nakai 1927 (—); 2. Matsui and Kumada 1928 (—)

Remarks: Although ayu are known to harbor this species (Nakai, 1927; Matsui and Kumada, 1928), no detailed information is available about its occurrence on ayu. According to Abe (1933), ayu in Taiwan are also infected with this species or a similar copepod (as "*Lernaeocera*").

Thersitina kasaharai (Do, 1981) Ohtsuka, Ho, Nagasawa, Morozinska-Gogol and Piasecki, 2004 (M or B)

Original combination: *Diergasilus kasaharai* Do, 1981

Sites of infection: [branchial cavity, gills]

Distribution: unknown

Record: Do 1982 (—)

Remarks: This species usually infects the grey mullet *Mugil cephalus* (Mugilidae) and is a marine or brackish-water parasite. It is thus thought that the fish examined by Do (1982) became infected by the copepod in marine coastal waters before migrating to fresh waters. Although Do (1982) did not give any information on the collection locality, it is most likely to be Kojima Bay (in the Seto Inland Sea) because he conducted various surveys in this bay. The copepod was recently transferred to the genus *Thersitina* (Ohtsuka et al., 2004).

Branchiura

Argulus coregoni Thorell, 1864 (FW)

Synonym: *Argulus plecoglossi* Yamaguti, 1937

Site of infection: body surface

Distribution: Nagano, Kyoto, Wakayama

Records: 1 Yamaguti 1937 (Kyoto: Hozu River); 2. Hoshina 1950 (Nagano: Akashina Fisheries Advisory Station); 3. Nagasawa and Ohya 1996 (Wakayama: Fisheries Laboratory of Kinki University)

Remarks: *Argulus plecoglossi* described by Yamaguti (1937) was regarded by Tokioka (1965) as a junior synonym of *A. coregoni*, and this view was supported by Shimura (1981).

Argulus japonicus Thiele, 1900 (FW)

Site of infection: [body surface]

Distribution: unknown

Record: Kobayashi 1938 (—)

Remarks: Kobayashi (1938) reported that this species infected ayu but provided no morphological description. Thus, the identification needs to be confirmed in comparison with *Argulus coregoni*.

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日本産アユの寄生虫目録（1912～2007年）

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要　旨　1912～2007年の96年間に出版された文献に基づき，日本産アユ *Plecoglossus altivelis altivelis* の寄生虫に関する情報を寄生虫－宿主リストに整理して目録を作成した。本目録には，29種の寄生虫（微胞子虫類１種，ミクソゾア類１種，吸虫類13種，単生類３種，条虫類１種，線虫類１種，鉤頭動物３種，カイアシ類４種，エラオ類２種）に加えて，学名がまだ決定していない寄生虫の情報が含まれる。寄生虫－宿主リストでは，各寄生虫は高位分類群ごとに配列され，最新の学名，シノニム，寄生部位，地理的分布および報告者の情報が示されている。アユの亜種，リュウキュウアユ *Plecoglossus altivelis ryukyuensis* からは寄生虫の記録はない。ミクソゾア類の *Mitraspora plecoglossi* を *Hoferellus* 属に移すとともに，ハスコウトウチュウ *Acanthocephalus opsariichthydis* Yamaguti, 1935の学名が動物命名規約に則って正しい綴りと命名年であることを確定した。また鉤頭動物の *Echinorhynchus oblitus* をカジカコウトウチュウ *Echinorhynchus cotti* のシノニムとした。

キーワード：アユ；寄生虫；目録；*Echinorhynchus oblitus*；*Hoferellus plecoglossi* n. com.；*Plecoglossus altivelis altivelis*