

Argulus coregoni (Crustacea: Branchiura: Argulidae) Parasitic on a Dark Chub *Nipponocypris temminckii* (Cypriniformes: Xenocyprididae) in a Stream, Central Japan, with a List of Its Known Hosts in East Asia

Kazuya Nagasawa^{1,2,4}, Ryu Uchiyama², and Ko Tomikawa³

¹ Graduate School of Integrated Sciences for Life, Hiroshima University,
1-4-4 Kagamiyama, Higashi-Hiroshima, Hiroshima 739-8528, Japan
E-mail: ornatus@hiroshima-u.ac.jp

² Aquaparasitology Laboratory, 365-61 Kusanagi, Shizuoka 424-0886, Japan

³ Graduate School of Humanities and Social Sciences, Hiroshima University,
1-1-1 Kagamiyama, Higashi-Hiroshima, Hiroshima 739-8524, Japan

⁴ Corresponding author

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An adult male specimen of *Argulus coregoni* Thorell, 1864 was collected from the body surface of a dark chub *Nipponocypris temminckii* (Temminck and Schlegel, 1846) at 15 m elevation in a small stream in central Japan. The specimen collected is herein described and corresponds well to the descriptions of *A. coregoni* from European and East Asian countries. This represents the first record for *A. coregoni* from a fish of the cypriniform family Xenocyprididae in Japan, where this species usually occurs in higher-elevation mountain streams and infects fishes in two salmoniform families (Salmonidae and Plecoglossidae). The male of *A. coregoni* is characterized by the presence of two protrusions adorned with small spines and a digitiform projection on the ventro- and dorsoposterior margins, respectively, of the coxa of the second leg and the abdominal lobes have pointed posterior ends. In addition to these morphological characters, the number of plumose setae on the posterior margin of the coxa of the first leg and the number of supporting rods in the sucker membrane of the first maxilla are useful for distinguishing *A. coregoni* from a morphologically similar congeneric species, *A. japonicus* Thiele, 1900, which parasitizes cypriniform fishes in Japan. Based on literature published between 1936 and 2023, this paper also gives a list of the hosts of *A. coregoni* reported from East Asia, including the Russian Far East, China, Malaysia, and Japan. To date, 31 species and three subspecies of fishes are known as hosts of this parasite in East Asia, and these fishes belong to 16 families and eight orders, which indicates that the species is not a host-specific parasite. In order to further understand the host utilization of *A. coregoni* in Japan, it is necessary to study its occurrence on fishes of various taxonomic groups in rivers of different lengths.

Key Words: parasitic crustacean, fish louse, redescription, host utilization, host list, new host record.

Introduction

Argulus coregoni Thorell, 1864 is one of the crustacean parasites found on freshwater fishes in Europe and Asia (Neethling and Avenant-Oldewage 2016). In Japan, Tokioka (1936) reported this species for the first time, and it has so far been documented mainly from salmoniform fishes belonging to two families (Salmonidae and Plecoglossidae). Because of its importance as a pathogen in fisheries and aquaculture of these fishes, various aspects of the biology of *A. coregoni* have been studied, such as the geographical distribution (summarized by Nagasawa and Yuasa 2020: fig. 3), egg deposition (Shimura and Egusa 1980), larval development (Shimura 1981), seasonal occurrence (Shimura 1983a), and impacts on host fishes (Shimura et al. 1983a, b; Shimura and Inoue 1984; Katahira et al. 2021). However, in Japan, *A. coregoni* has also been reported from non-salmoniform fishes, which are placed in three families and three orders, and they are: bitterlings *Acheilognathus* sp. and

Tanakia limbata (Temminck and Schlegel, 1846) (Cypriniformes: Acheilognathidae) [Tokioka 1936; Nagasawa and Taniguchi 2021; see Goda et al. (2017) for the scientific name of the host reported by Tokioka (1936)]; fluvial dark sleeper *Odontobutis hikimius* Iwata and Sakai, 2002 (Gobiiformes: Odontobutidae) (Nagasawa et al. 2014); and torrent catfish *Liobagrus reinii* Hilgendorf, 1878 (Siluriformes: Amblycipitidae) (Nagasawa and Ishikawa 2015). Little is known about the biology of *A. coregoni* infecting these non-salmoniform fishes in Japan.

Recently, we collected an adult male specimen of *A. coregoni* from a dark chub *Nipponocypris temminckii* (Temminck and Schlegel, 1846) (Cypriniformes: Xenocyprididae) in a small stream in central Japan. This represents the first record for *A. coregoni* from the cypriniform family Xenocyprididae in Japan. However, a congeneric species, *A. japonicus* Thiele, 1900 has been reported from 11 species of cypriniform fishes in Japan, comprising five species of the Xenocyprididae [lakeweed chub *Ischikauia steenackeri* (Sauvage, 1883); freshwater minnow *Opsariichthys platy-*

pus (Temminck and Schlegel, 1846); three-lips *Op. uncirostris* (Temminck and Schlegel, 1846); silver carp *Hypophthalmichthys molitrix* (Valenciennes, 1844); and bighead carp *Hy. nobilis* (Richardson, 1845)] (e.g., Kimura 1970; Nagasawa 2009, 2011, 2017a, 2023a; Nagasawa and Sato 2014; Nagasawa and Miyajima 2018; Nagasawa et al. 2018a, 2021a, 2023a), one species of the Acheilognathidae [rosy bitterling *Rhodeus ocellatus* (Kner, 1866)] (Yamauchi and Shimizu 2013; Nagasawa et al. 2024a), one species of the Leuciscidae [big-scaled redbfin *Pseudaspius hakonensis* (Günther, 1877)] (Nagasawa et al. 2024b), and four species of the Cyprinidae (common carp *Cyprinus carpio* Linnaeus, 1758; goldfish *Carassius auratus* Linnaeus, 1758; Japanese white crucian carp *Car. cuvieri* Temminck and Schlegel, 1846; and silver crucian carp *Carassius* sp.) (e.g., Nakazawa 1914; Tokioka 1936; Yamaguti 1937; Kimura 1970; Takeda et al. 2000; Nagasawa et al. 2009, 2012, 2013, 2023b; Nagasawa and Nagai 2023). This indicates that Japanese cypriniform fishes are more often utilized by *A. japonicus* than *A. coregoni*, and Tokioka (1965) stated that both species of *Argulus* O. F. Müller, 1785 are morphologically very similar. Moreover, Nagasawa and Taniguchi (2021) mentioned that it is not easy to differentiate *A. coregoni* from *A. japonicus* by their gross morphology and, for accurate, reliable species identification, it is necessary to examine other characters, such as the number of plumose setae on legs and that of supporting rods in the first maxillae. Thus, when argulid specimens are collected from cypriniform fishes in Japan, it is important to carefully identify them based on several morphological characters. However, *A. coregoni* infecting Japanese cypriniform fishes has so far been poorly studied for its morphology, and there are two descriptions of the species only from bitterlings (Acheilognathidae) (Tokioka 1936; Nagasawa and Taniguchi 2021).

Based on this background, we report on the morphology of *A. coregoni* using the male specimen from the xenocypridid fish (dark chub) and mention the necessity for future research to assess the importance of non-salmoniform fishes as hosts of this parasite in Japan. Dark chub represents a new host record for *A. coregoni*, and based on litera-

ture published between 1936 and 2023, a list is given of the known hosts of this parasite in East Asia.

Materials and Methods

About 100 individuals of dark chub were collected with a plastic bottle trap in the middle reaches of the Takase River (ca. 5 m river width, ca. 1 m water depth, 15 m elevation; Fig. 1A) at Tsuzurafuchi in Shirahama, Wakayama Prefecture, central Japan, on 21 September 2021. This river is a short stream (ca. 7.7 km length) and joins the Tonda River which drains downstream at 0.2 km into the western North Pacific Ocean. Soon after capture, these fish were transported alive to a tank at the second author's house, and one of them (ca. 70 mm total length) was found to be infected with a crustacean parasite on the dorsal body surface (Fig. 1B). This parasite was carefully taken from the fish, fixed, and then preserved in 70% ethanol. Later, at the Aquaparasitology Laboratory, Shizuoka Prefecture, the specimen was examined using an Olympus SZX10 stereo microscope and an Olympus BX51 phase-contrast compound microscope. It was cleared in lactophenol and observed using the wooden slide procedure (Humes and Gooding 1964; Benz and Otting 1996). All drawings were made with the aid of drawing tubes attached to the microscopes. Morphological terminology follows Benz et al. (1995) and Benz and Otting (1996).

Data on the elevation (m) at the collection sites reported in this and previous papers (Nagasawa and Taniguchi 2021) were obtained from a GSI map (<https://maps.gsi.go.jp/>) provided by the Geospatial Information Authority of Japan. The scientific names of fishes from Japan and other countries mentioned in this paper follow Motomura (2023) and Froese and Pauly (2023), respectively. The order and family, to which each fish species belongs, is based on Froese and Pauly (2023). The specimen of *A. coregoni* has been deposited in the Crustacea collection of the National Museum of Nature and Science, Tsukuba, Ibaraki Prefecture, Japan (NSMT-Cr).

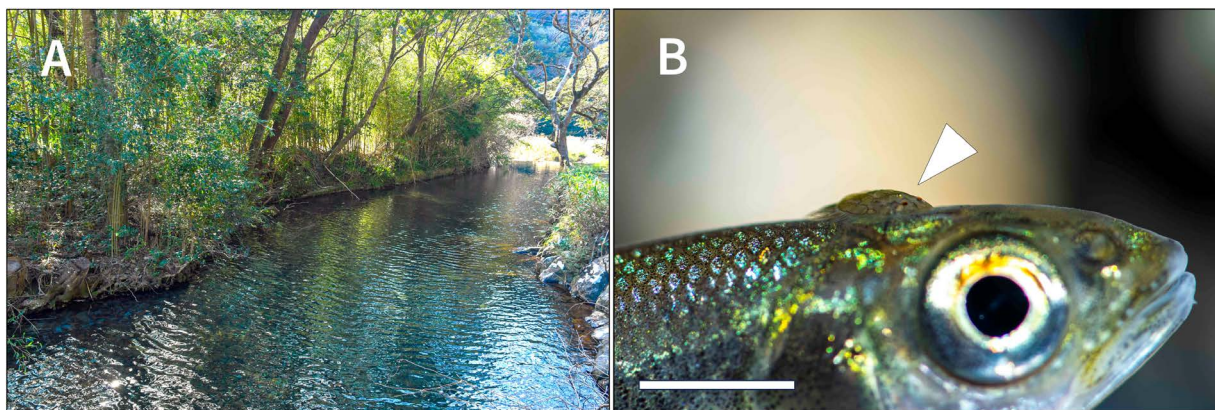


Fig. 1. *Argulus coregoni* and its collection site. A, Middle reaches of the Takase River where dark chub were collected; B, a dark chub (ca. 70 mm total length) infected with an adult male of *A. coregoni* (arrowhead) on the dorsal body surface at the boundary between the head and trunk. Scale bar: 5 mm.

Results

Argulus coregoni Thorell, 1864

[Japanese name: Chou-modoki (Tokioka 1965)]

(Figs 1B, 2–5)

Material examined. One adult male (NSMT-Cr 31596).

Adult male. *Body* dorsoventrally flattened, measuring 4.2 mm in total length (from anterior tip of carapace to posterior tip of abdomen) and 2.5 mm in maximum body width (around midlength of carapace).

Carapace (including posterolateral lobes) nearly circular, covering totally or almost totally coxa and basis of first to third pairs of legs and partially fourth pair of legs in dorsal view; 3.0 mm long, comprising 71.4% of total length (Figs 2, 5). Frontal region of carapace delimited by anterolateral indentations and protruding anteriorly; anterior margin rounded. Central longitudinal ribs distinct and bifurcated at anterior ends; transverse ribs evident behind nauplius eye (Fig. 2A). Paired compound eyes well visible, dorsally located at level of anterolateral indentations of carapace (Fig. 2A). Nauplius eye located posterior to compound eyes in midline of carapace. Dorsal surface of carapace smooth without spines. Ventral surface of frontal and anterolateral regions of carapace ornamented with numerous, small posteriorly directed spines (Fig. 2B). Posterolateral lobes of carapace not overlapping, ending in rounded margin, separated by sinus 26.7% as long as carapace (Fig. 2A). Respiratory areas located at level between second maxillae and third

pairs of legs; smaller anterior area nearly oval, located near anterior margin of posterior area; larger posterior area kidney-shaped, with notch on mesial margin (Figs 2B, 3A, 5). *Thorax* with four segments, bearing small spiniform projections ventrally (Figs 2, 5). *Abdomen* longer than wide, with some, very small spines on anterolateral margins; anal indentation 44.4% as long as abdomen to form two lobes; each lobe becoming wider toward mid-length of abdomen, then tapering posteriorly, ending in pointed margin (Figs 2, 5). Paired testes each elliptical, located in antero-central portion of abdomen, extending past base of anal indentation (Figs 2, 5). Caudal rami located at base of anal indentation, with four naked setae on posterior margin of each ramus (Figs 2A, 3B).

First antennae with four segments (Fig. 3C, D): first segment heavily sclerotized in mesial and posterior regions, with large blunt projection on posterior margin; second segment largest and heavily sclerotized, with large blunt projection on anterior margin, strong lateroventrally directed hook at distal corner, and large projection ventrally near posterior margin; third segment cylindrical, with three naked setae; apical segment shorter than third segment, with four and two naked setae near and at tip, respectively. *Second antennae* with five segments (Fig. 3C, E): first segment sclerotized, with large blunt projection and small swelling bearing six naked setae on posterior margin, and small spine near distal margin; second segment shorter than first, armed with four naked setae on posterior margin and three naked setae near distal margin; third, fourth, and apical segments nearly cylindrical and decreasing in length;

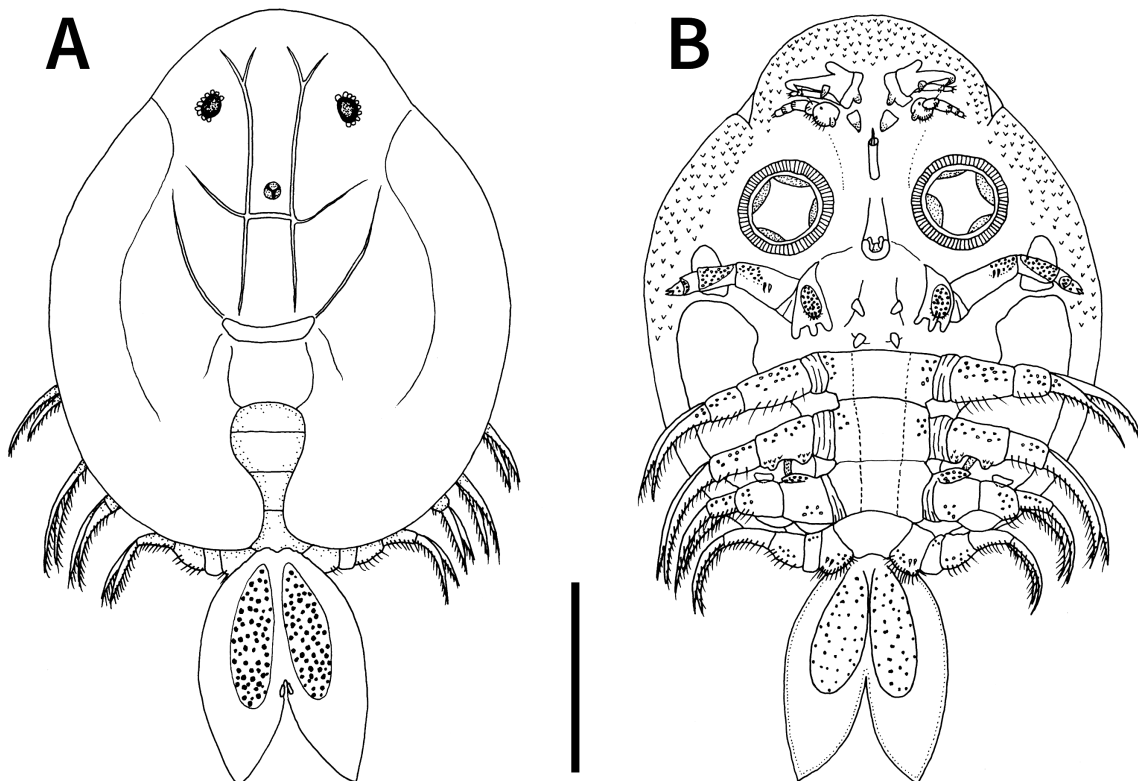


Fig. 2. *Argulus coregoni*, adult male, NSMT-Cr 31596. A, Habitus, dorsal view; B, habitus, ventral view. Scale bar: 1 mm.

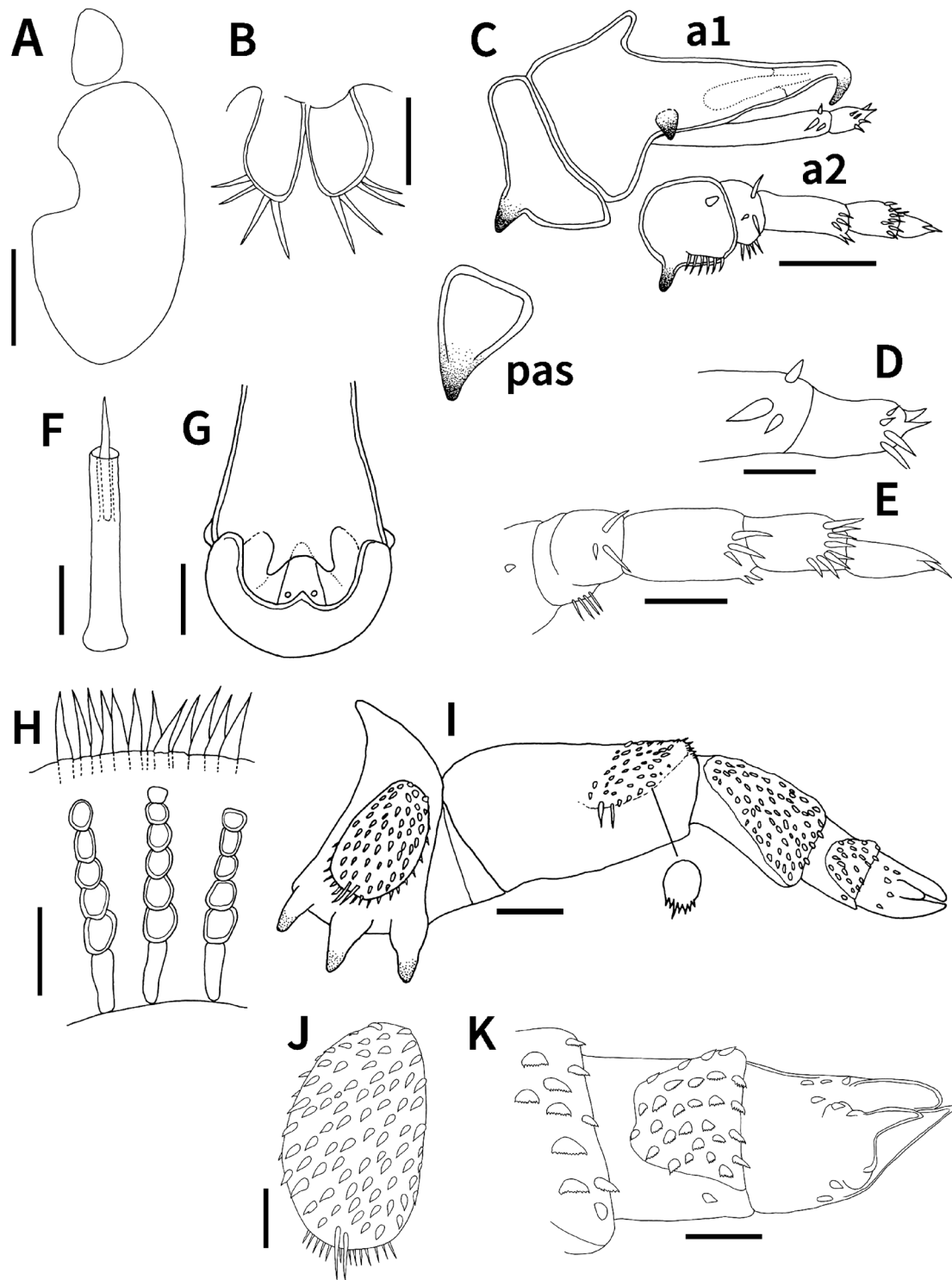


Fig. 3. *Argulus coregoni*, adult male, NSMT-Cr 31596. A, Respiratory areas, ventral view; B, caudal rami, ventral view; C, first antenna (a1), second antenna (a2), and postantennal spine (pas), ventral view; D, third and apical segments of first antenna, ventral view; E, second, third, fourth, and apical segments of second antenna, ventral view; F, preoral sheath and stylet, ventral view; G, mouth tube, ventral view; H, three anterior supporting rods and marginal projections from rim of first maxilla sucker, ventral view; I, second maxilla and denticle (enlarged) on second segment, ventral view; J, raised field on first segment of second maxilla, ventral view; K, third, fourth, and terminal segments of second maxilla, ventral view. Scale bars: A, 0.2 mm; B, E–G, J, K, 0.05 mm; C, I, 0.1 mm; D, H, 0.03 mm.

third segment with three naked and two short naked setae near distal margin; fourth segment with eight naked setae near distal margin; apical segment with three naked setae at tip. Postantennal spines large and robust, each located posterior to projection of first segment of first antenna (Fig.

3C). Preoral sheath cylindrical and visible on ventral mid-line of carapace posterior to postantennal spines; anterior portion of stylet protruding from opening of preoral sheath (Figs 2B, 3F). Mouth tube without ornamentation located posterior to preoral sheath, becoming wider posteriorly;

posterior portion composed of anterior labrum and posterior labium bearing pair of tiny spines (Figs 2B, 3G).

First maxillae forming well developed cup-like suckers (Fig. 2B), each with 60 supporting rods in sucker membrane. Supporting rods each composed of six or seven sclerites; sclerites at base nearly oblong but others oval or slightly trapezoidal and decreasing in size distally (Fig. 3H). Outer margin of rim of sucker membrane ornamented with numerous apically pointed projections. **Second maxillae** with five segments (Fig. 3I): first segment robust, with three large, blunt, almost equally long projections on posterior margin; corpus of first segment with raised oval field bearing many denticles plus two long and 14 shorter naked setae near and on posterior margin, respectively (Fig. 3J); second segment longer than first, with two long naked setae and denticles (some with serrated margin) on distal portion of anteroventral surface (Fig. 3I); third segment shorter and narrower than second segment, with field bearing many denticles with serrated margin on anteroventral surface; fourth segment subquadrate, with small field bearing denticles with serrated margin; terminal segment shortest with several denticles, ending in three projections (one is blunt and two are pointed apically) (Fig. 3K). Accessory spines near ventral midline, each located slightly apart from first segment of second maxilla (Fig. 2B). Postmaxillary spines small, each located anterior to first segment of thorax (Fig. 2B).

First to fourth pairs of legs (Fig. 4) biramous with sympods two-segmented, each composed of coxa and basis; rami each consisting of exopod and endopod; sympods and rami of first to fourth legs ventrally covered with small, simple cuticular scales; rami bearing two rows of plumose setae each near ventro- or dorsoposterior margin; first and second pairs of legs each possessing flagellum projecting from base of exopod. **First leg** (Fig. 4A, B) coxa bearing six plumose setae near ventroposterior margin; basis nearly half as wide as coxa, bearing four plumose setae near ventroposterior margin; exopod unsegmented, with 16 ventral plumose setae; endopod three-segmented, proximal segment long, with 12 ventral plumose setae and one short naked seta, middle segment much shorter than proximal segment, and terminal segment tapering distally, ending in two short spines; flagellum extending to proximal margin of coxa, with 17 plumose setae on ventroposterior margin. **Second leg** (Fig. 4C, D) coxa with two protrusions adorned with small, apically truncated spines on ventroposterior margin and posteriorly directed digitiform projection on dorsoposterior margin; basis slightly shorter than coxa, bearing four plumose setae near ventroposterior margin; exopod and endopod unsegmented, with two rows of plumose setae (15 and 17 ventral setae on exopod and endopod, respectively); flagellum extending to proximal margin of coxa, with 16 plumose setae on ventroposterior margin. **Third leg** (Fig. 4E, F) coxa with irregularly shaped, raised fields adorned with denticles on anterior and dorsal surface; basis slightly shorter than coxa, bearing raised disk-shaped field covered with denticles on anterior surface and three plumose setae near ventroposterior margin; large swelling (= socket) present on posterior margin of coxa and basis; exopod unsegmented,

with 21 plumose setae near ventroposterior margin; endopod two-segmented, proximal segment with seven plumose setae near ventroposterior margin, terminal segment with nine plumose setae near ventroposterior margin. **Fourth leg** (Fig. 4G, H) coxa forming natatory lobe, bearing 15 plumose setae on posterior margin and two short naked setae near ventroposterior margin; basis with peg on anterior margin and six plumose setae on posterior distal margin; peg bearing pair of triangular-shaped processes on antero-distal surface and ending in three spines (one heavily ornamented with minute processes); exopod unsegmented, bearing 17 plumose setae near ventroposterior margin; endopod two-segmented, proximal segment with seven plumose setae near ventroposterior margin and short naked seta near posterodistal corner, and terminal segment with nine plumose setae near ventroposterior margin.

Color. When fresh, body almost transparent; compound eyes and naupliar eye dark brown; respiratory areas fringed by dark brown pigment; central portion of third segment of trunk black; black spots scattered on pale-yellow testes (Fig. 5A). In 70% ethanol (the specimen was fixed on 21 September 2021 and observed on 20 July 2022), body white; compound eyes and naupliar eye black; outline of respiratory areas recognized ventrally by dark brown pigment; black spots scattered on pale-yellow testes (Fig. 5B, C).

Host. Dark chub *Nipponocypris temminckii* (Cypriniformes: Xenocypridae).

Attachment site. Dorsal body surface at the boundary between the head and trunk (Fig. 1B). The individual of *A. coregoni* was found to be oriented anteriorly.

Locality. The middle reaches of the Takase River (33°39'04"N, 135°25'14"E, 15 m elevation; Fig. 1B), a tributary of the Tonda River, at Tsuzurafuchi in Shirahama, Wakayama Prefecture, central Japan.

Remarks. *Argulus coregoni* was originally described by Thorell (1864) based on specimens collected from three species of salmonids, i.e., European whitefish *Coregonus lavaretus* (Linnaeus, 1758) (reported as *Coregono lavareto*), grayling *Thymallus thymallus* (Linnaeus, 1758) (as *Thymallo vulgari*), and sea trout *Salmo trutta* Linnaeus, 1758 (as *Salmone trutta*), in Sweden. This parasite has since been reported from European countries, including Sweden (Thorell 1866), Norway (Økland 1985; Bristow 1993; Dolven 2020), Finland (e.g., Pasternak et al. 2004; Mikheev et al. 2007, 2015; Bandilla et al. 2008; Hakalahti-Sirén et al. 2008), Russia (Markevich 1937; Gusev 1987), Poland (Penczak 1972), the Czech Republic and the Slovak Republic (Romanovský 1955; Moravec 2001), Germany (Wagler 1935; Stammer 1959), France (Roland 1963), and the U.K. (Martin 1932; Gurney 1948; Rizvi 1969; Campbell 1971; Fryer 1982; Taylor et al. 2006). The species is also known to occur in East Asia, including the Russian Far East (Markevich 1937; Dogiel and Akhmerov 1952; Smirnova 1971; Gusev 1987; Ermolenko and Kazachenko 1989; Ermolenko 1992, 2004a, b; Sokolov et al. 2012), China (Wang 1958, 1964; Yin 1962; Chen 1973; Ding 1977; Song and Kuang 1980; Kuang and Qian 1991; Zang and Ma 1994; Yue et al. 1997; Wadeh et al. 2008), Malaysia (Everts and Avenant-Oldewage 2009), and Japan

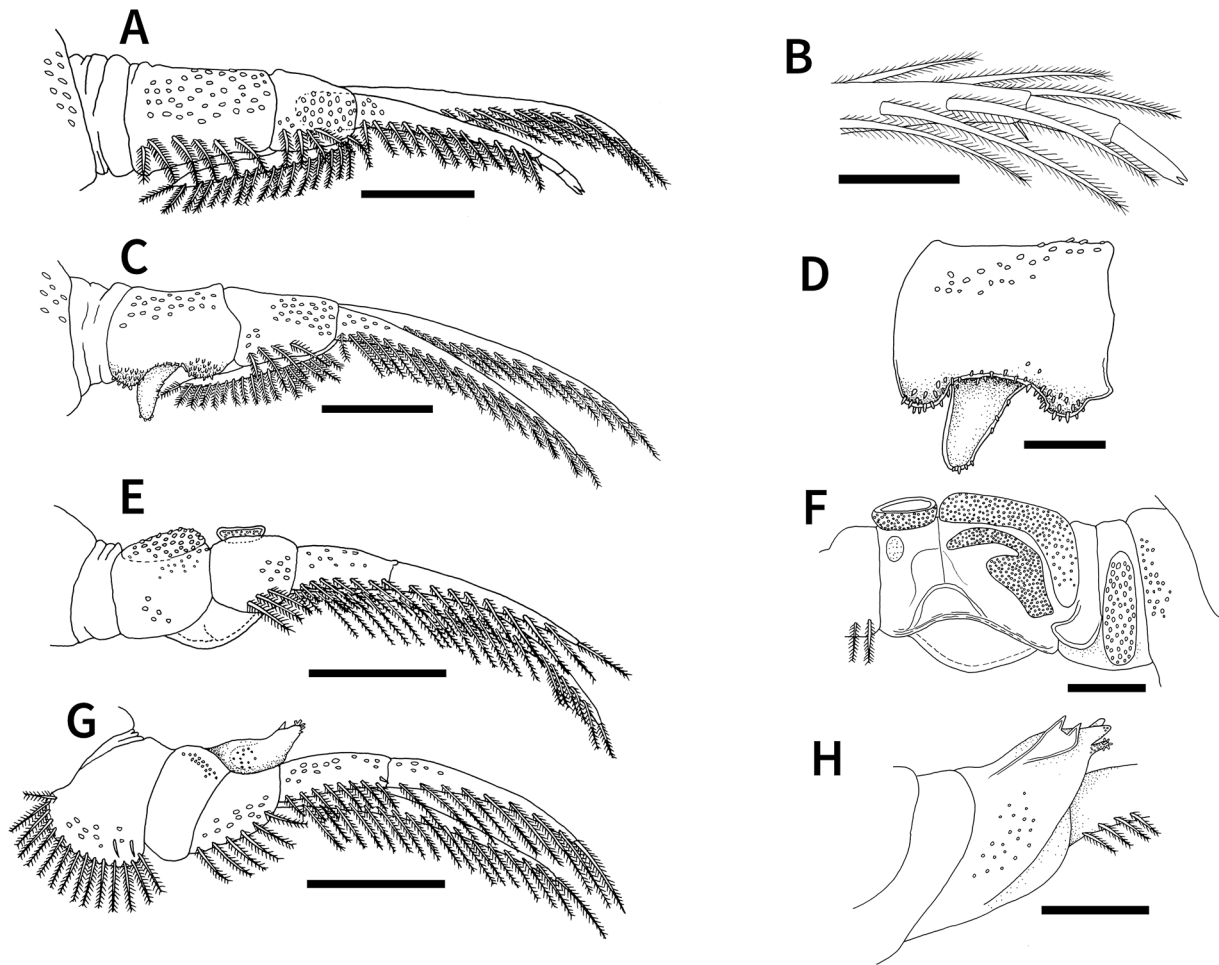


Fig. 4. *Argulus coregoni*, adult male, NSMT-Cr 31596. A, First leg, ventral view; B, distal part of endopod of first leg, ventral view; C, second leg, ventral view; D, coxa of second leg, ventral view; E, third leg, ventral view; F, coxa, base, and part of exopod of third leg, dorsal view; G, fourth leg, ventral view; H, base (with peg) and part of endopod of fourth leg, anteroventral view. Scale bars: A, C, E, G, 0.3 mm; B, D, F, H, 0.1 mm.

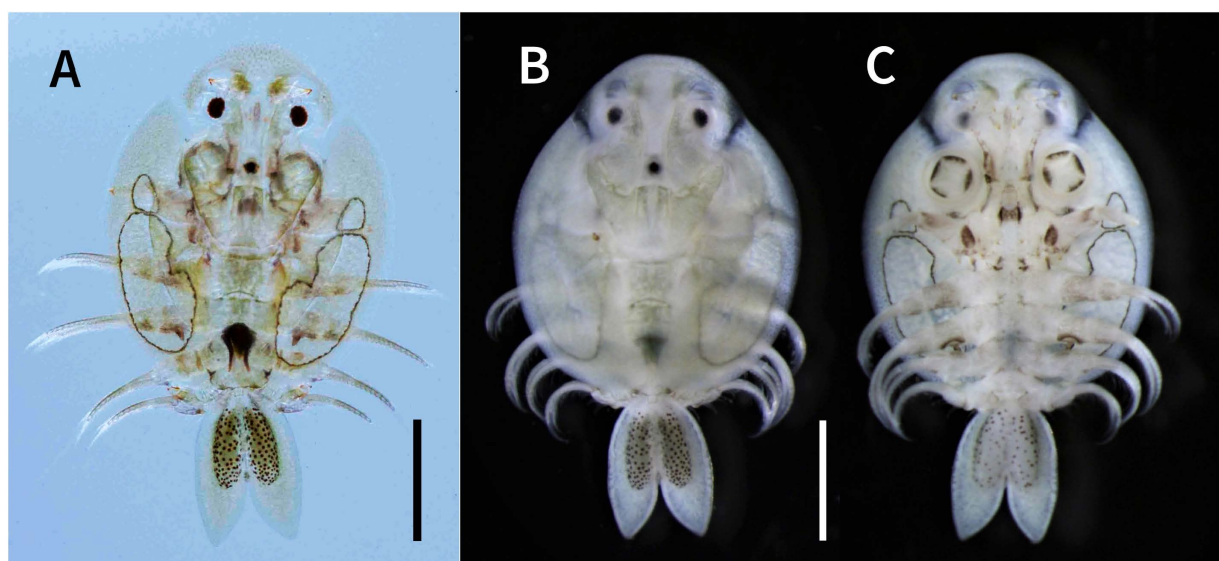


Fig. 5. *Argulus coregoni*, adult male, NSMT-Cr 31596. A, Habitus, fresh specimen, dorsal view; B, C, habitus, ethanol-preserved specimen, dorsal and ventral views, respectively. The specimen was fixed in 70% ethanol on 21 September 2021 and photographed on 20 July 2022. Scale bars: 1 mm.

(see below). Moreover, *A. coregoni* was reported from India (Saha and Bandyopadhyay 2015; Khwaja and Tripathi 2022) and Pakistan (Khan et al. 2017), South Asia, and from Iran (Mousavi et al. 2011), West Asia, but since its morphology was not studied in detail, a reassessment of the identification of the species from these countries is necessary.

In Japan, *A. coregoni* has been described mainly from specimens taken from fishes in the two salmoniform families (Salmonidae and Plecoglossidae) (Yamaguti 1937; Hoshina 1950). Yamaguti (1937) described a new species (*Argulus plecoglossi* Yamaguti, 1937) from ayu *Plecoglossus altivelis altivelis* (Temminck and Schlegel, 1846) (Plecoglossidae), but it has been regarded as a junior synonym of *A. coregoni* (Tokiooka 1965; Shimura 1981: 347). In contrast to this, there is limited information on the morphology of *A. coregoni* from cypriniform fishes, and its specimens have only been collected from bitterlings (Acheilognathidae) (Tokiooka 1936; Nagasawa and Taniguchi 2021).

The morphological characters of the specimen collected from dark chub (Xenocyprididae) in this study corresponds to the descriptions of the male of *A. coregoni* from European countries (Thorell 1864; Thiele 1904; Gurney 1948; Romanovský 1955; Stammer 1959; Roland 1963; Penczak 1972; Fryer 1982), China (Wang 1958; Chen 1973; Kuang and Qian 1991), Malaysia (Everts and Avenant-Oldewage 2009), and Japan (Tokiooka 1936; Yamaguti 1937; Hoshina 1950), and the specimen is thus identified as *A. coregoni*. The male of this species is characterized by the presence of two protrusions adorned with small spines and a digitiform projection on the ventro- and dorsoposterior margins, respectively, of the coxa of the second leg (Fig. 4C, D) and the abdominal lobes have pointed posterior ends (Figs 2, 5). These characters were clearly recognizable in the original description of *A. coregoni* (Thorell 1864: figs 2, 10, 15). Regarding the dorsal digitiform projection, Tokiooka (1936: fig. 3) reported that it is “very long” and actually illustrated a long projection, which is similar to that of our specimen (Fig. 4D). The Chinese specimens have also a similar long dorsal projection (Chen 1973: fig. 216; Kuang and Qian 1991: fig. 98D). Nevertheless, there are some variations in the second leg morphology between the specimens reported in other regions. In the European specimens, a well-developed dorsal projection was recognized by Thiele (1904: fig. 86), Romanovský (1955: fig. 32) and Penczak (1972: fig. 13) but not by Fryer (1982: fig. 92). Roland (1963: fig. 6A, B) illustrated only two protrusions. The Malaysian specimens have a short dorsal projection and two ventral protrusions (reported as projections) of different sizes (Everts and Avenant-Oldewage 2009: fig. 10).

Although only one male specimen of *A. coregoni* was collected in this study, there are several morphological differences between the sexes of the species. The male has accessory copulatory structures, i.e., two protrusions and a digitiform projection on the coxa of the second leg, a large swelling (= socket) on the coxa and basis of the third leg, and the peg on the basis of the fourth leg (Fig. 4C–H), all of which are not present in the female (Nagasawa 2021: fig. 2). In addition, black spots are found on the surface of the tes-

tes (Figs 2, 5; Thorell 1864: fig. 2; Hoshina 1950: fig. 1A; Romanovský 1955: fig. 35; Roland 1963: fig. 2; Penczak 1972: fig. 2; Nagasawa and Kawai 2008: fig. 1).

The flagella are known to project each from the extreme proximal part of the exopod of both the first and second pairs of legs in branchiurans of the genus *Argulus* (Boxshall and Jaume 2009). In this study, we have confirmed that the flagella project at the base of the exopod of the first and second legs in *A. coregoni* (Fig. 4A, C). In Japan, such flagella have been reported from three other congeneric species, i.e., *A. japonicus* (Nagasawa 2021), *A. mongolianus* Tokiooka, 1939 (Nagasawa et al. 2022a), and *A. nobilis* Thiele, 1904 (Nagasawa 2023b).

In this study, we collected the specimen of *A. coregoni* from dark chub (*N. temminckii*) in a stream in Wakayama Prefecture, central Japan. Dark chub is distributed in central and western Japan and the southwestern region of the Korean Peninsula (Hosoya 2015), but there is no record of *A. coregoni* from this fish species elsewhere in Japan or in Korea. Thus, dark chub is herein regarded as a new host of *A. coregoni*. There are five previous records of this parasite from Wakayama Prefecture, where it infects red-spotted masu salmon *Oncorhynchus masou ishikawae* Jordan and McGregor, 1925 [reported as *Salmo* (On.) *masou macrostomus* (Günther, 1877)] in the Hiki River near the Takase River (Takegami 1984) and also reared red-spotted masu salmon (reported as *On. mas. ishikawai*), rainbow trout *On. mykiss* (Walbaum, 1792) (reported as *Salmo irideus* Gibbons, 1855), and ayu *Pl. a. altivelis* (reported as *Pl. altivelis*) (Hoshina 1950; Nagasawa and Ohya 1996a, b; Kaji et al. 2011).

The specimen of *A. coregoni* was found attached on the dorsal body surface at the boundary between the head and trunk of the dark chub (Fig. 1B). A similar attachment site was also reported in the same species of parasite infecting oily bitterling *Tan. limbata* from the Asahi River, Okayama Prefecture (Nagasawa and Taniguchi 2021: fig. 1). This may indicate that, in these cypriniform fishes, the anterior, dorsal body surface is commonly used by *A. coregoni* as its attachment site. Nonetheless, in salmonids inhabiting mountains streams in central Japan, this parasite is also found on the lateral body surface under and near the pectoral fins (Nagasawa et al. 2022b). This use of the pectoral fin area by *A. coregoni* may be associated with the hosts' habitat. Because salmonids usually occur in fast-flowing streams, it has been inferred that this parasite uses such an area as a shelter to lessen the chance of being detached from the host (Shimura 1983a; Nagasawa et al. 2022b).

As stated above, the male of *A. coregoni* examined in this study has a posteriorly directed digitiform projection on the dorsoposterior margin of the coxa of the second leg (Fig. 4C, D). Despite its size variation, a similar projection has been recognized in the male of the species in Europe and East Asia, and it is regarded as the morphological feature that characterizes *A. coregoni*. In contrast, the male of *A. japonicus* is morphologically similar to *A. coregoni* but has no such digitiform projection (Tokiooka 1936: fig. 2; Yamaguti 1937: fig. 8; Chen 1973: fig. 194; Fryer 1982: fig. 94; Kuang

and Qian 1991: fig. 100D). Thus, the presence or absence of the digitiform projection on the second leg can be used in identification of males of these congeneric species.

In addition, for identification of both sexes of *A. coregoni* and *A. japonicus*, the number of plumose setae on the posterior margin of the coxa of the first leg and the number of supporting rods in sucker membrane of the first maxilla are useful (Nagasawa and Taniguchi 2021). Based on observations in Japan, the number of plumose setae ranges from four to nine in *A. coregoni* [four to seven in Yamaguti (1937); four to nine in Hoshina (1950); six in Nagasawa and Taniguchi (2021); six in this study], whereas it is constantly one in *A. japonicus* (Yamaguti 1937; Nagasawa 2021). The number of supporting rods per first maxilla is usually 60 or more in *A. coregoni* [ca. 60 in Tokioka (1936); 60–70 in Yamaguti (1937); 54–73 in Hoshina (1950); 67 and 72 in Nagasawa and Taniguchi (2021); 60 in this study], but it ranges from 40 to 52 in *A. japonicus* [ca. 50 in Tokioka (1936); 40–50 in Yamaguti (1937); 50 and 52 in Nagasawa (2021)]. A similar difference in the number of supporting rods per first maxilla between the two species has been reported from China as well [64 and 71 (Wang 1958) and 68 (Chen 1973; Kuang and Qian 1991) in *A. coregoni*; 50 (Wang 1958) and 43–46 (Chen 1973; Kuang and Qian 1991) in *A. japonicus*]. The Malaysian specimens of *A. coregoni* have ca.

62 supporting rods (Everts and Avenant-Oldewage 2009).

There is a paper on argulid branchiuran identified as “*A. japonicus*” from Malaysia (Seng 1986), but its leg structure does not correspond to that of *A. japonicus*. The Malaysian specimens had seven setae on the posterior margin of the coxa of the first leg and three protrusions (reported as knobs, two are ventral but one is dorsal) on the posterior margin of the coxa of the second leg (Seng 1986: figs 18, 20). As stated above, these characters are identical to the leg morphology of *A. coregoni*. When Everts and Avenant-Oldewage (2009) later reported *A. coregoni* as a new country record from Malaysia, they did not mention that the species had been misidentified before. Seng (1986) suggests that *A. coregoni* (reported as *A. japonicus*) has been widely spread in Malaysia.

Discussion

Recently, we have conducted a study on the longitudinal distribution patterns of *A. coregoni* in rivers in Gifu and Shiga prefectures, central Japan (Nagasawa et al. 2022b; Nagasawa 2023c). The surveyed rivers were large ones that originate from high-elevation mountain areas and drain into the seas or Lake Biwa (the largest lake in Japan), and

Table 1. Hosts of *Argulus coregoni* reported in the Russian Far East. The classification scheme and scientific names of fishes are adopted from Froese and Pauly (2023). Fishes are alphabetically arranged in each family.

Host			Locality		Reference
Order	Family	Species	Province	Site	
Salmoniformes	Salmonidae	<i>Hucho taimen</i>	Amur Oblast and Khabarovsk Krai	Amur River basin (including the Zeya River and Lake Khivanda)	Smirnova (1971)
		<i>Oncorhynchus gorbuscha</i>	Khabarovsk Krai	Amur River basin (Lake Udył)	Dogiel and Akhmerov (1952)
		<i>Oncorhynchus keta</i>	Khabarovsk Krai	Amur River basin (Lake Udył)	Dogiel and Akhmerov (1952)
Cypriniformes	Cyprinidae	<i>Carassius gibelio</i>	Amur Oblast and Khabarovsk Krai	Amuri River basin (including the Zeya River and Lake Khivanda)	Smirnova (1971) (as <i>Car. auratus gibelio</i>)
		<i>Cyprinus carpio</i>	Amur Oblast and Khabarovsk Krai	Amur River basin (including the Zeya River and Lake Khivanda)	Smirnova (1971) (as <i>Cy. haematopterus</i>)
		<i>Cyprinus</i> sp.	Khabarovsk Krai	Amur River basin	Dogiel and Akhmerov (1952)
	Gobionidae	<i>Gobio soldatovi</i>	Khabarovsk Krai Sakhalin	Amur River basin Sweet Lake	Dogiel and Akhmerov (1952) (as <i>Go. gobio</i>) Sokolov et al. (2012)
		<i>Pseudorasbora parva</i>	Primorsky Krai	Razdolnaya River basin —*	Ermolenko and Kazachenko (1989) Ermolenko (1992)
	Nemacheilidae	<i>Barbatula toni</i>	Primorsky Krai	Razdolnaya River basin	Ermolenko (2004a) (as <i>Nemachilis barbatus toni</i>)
	Siluridae	<i>Silurus asotus</i>	Amur Oblast and Khabarovsk Krai	Amur River basin (including the Zeya River and Lake Khivanda)	Smirnova (1971) (as <i>Parasilurus asotus</i>)
Siluriformes	Bagridae	<i>Tachysurus fulvidraco</i>	Sakhalin	Sweet Lake	Sokolov et al. (2012)
Esociformes	Esocidae	<i>Esox reichertii</i>	Khabarovsk Krai Sakhalin	Amur River basin Sweet Lake	Dogiel and Akhmerov (1952) (as <i>E. reicherti</i>) Sokolov et al. (2012)
		<i>Percottus glenii</i>	Primorsky Krai	Razdolnaya River basin Bolshoe Mramornoe Lake —	Ermolenko and Kazachenko (1989) (as <i>Pe. glehni</i>), Ermolenko (2004b) (as <i>Pe. glehni</i>) Ermolenko and Kazachenko (1989) (as <i>Pe. glehni</i>), Ermolenko (2004b) Ermolenko (1992) (as <i>Pe. glehni</i>)
Unknown	Unknown	Unknown	Unknown	Amur River basin	Markevich (1937)

* Not reported.

we have revealed that salmonids and ayu serve as important hosts for *A. coregoni* in the upper and middle-lower reaches of rivers, respectively. However, the fish fauna in Japanese rivers, especially those in central and western Japan, does not consist of only salmonids and ayu but also fish species belonging to other taxonomic groups and, in particular, cypriniform fishes are abundant in the middle and lower reaches (e.g., Matsumiya et al. 2001; Hirayama and Nakagoshi 2003; Nitta et al. 2014; Ishizaki et al. 2016), and the number of fish species per river is affected by the river

length (e.g., Hirayama and Nakagoshi 2003). Moreover, as stated in the Introduction, *A. coregoni* has been reported from non-salmoniform fishes (those belonging to three orders: Cypriniformes, Gobiiformes, and Siluriformes) as well. Therefore, in order to further understand the host utilization of *A. coregoni* in Japanese rivers, it is important to study its occurrence on fishes of various taxonomic groups in rivers of different lengths.

In this study, we collected *A. coregoni* from a cypriniform fish (dark chub) in the middle reaches of a short stream (the

Table 2. Hosts of *Argulus coregoni* reported in China. The classification scheme and scientific names of fishes are adopted from Froese and Pauly (2023). Fishes are alphabetically arranged in each family.

Host			Locality		Reference
Order	Family	Species	Province	Site	
Acipenseriformes	Acipenseridae	<i>Huso dauricus</i>	—*	—	Kuang and Qian (1991)
Cypriniformes	Cyprinidae	<i>Carassius auratus</i>	Inner Mongolia	Ulanusuhai Nur	Yin (1962)
			Sichuan	Various sites	Ding (1977)
			—	Four sites	Zang and Ma (1994)
			—	—	Kuang and Qian (1991)
	Xenocyprididae	<i>Cyprinus carpio</i>	Inner Mongolia	Ulanusuhai Nur	Yin (1962)
			Sichuan	Various sites	Ding (1977)
		<i>Mylopharyngodon piceus</i>	—	Four sites	Zang and Ma (1994)
			—	—	Kuang and Qian (1991)
			Xinjiang Uygur Autonomous Region	Two sites	Yue et al. (1997)
			—	—	Kuang and Qian (1991) (as <i>Ct. idellus</i>)
Siluriformes	Siluridae	<i>Silurus asotus</i>	Jiangsu	Suzhou	Wang (1958) (as <i>M. aethiops</i>), Wang (1964)
			Sichuan	Various sites	Ding (1977)
	Bagridae	<i>Tachysurus fulvidraco</i>	—**	Four sites	Zang and Ma (1994)
			—	—	Song and Kuang (1980)
			—	—	Kuang and Qian (1991)
			—	—	—
Centrarchiformes	Sinipercaidae	<i>Siniperca chuatsi</i>	Inner Mongolia	Ulanusuhai Nur	Yin (1962) (as <i>Parasilurus asotus</i>)
			—	—	Kuang and Qian (1991) (as <i>Pa. asotus</i>)
			Jiangsu	Various sites	Wang (1964) (as <i>Pseudobagrus fulvidraco</i>)
			Sichuan	Four sites	Zang and Ma (1994) (as <i>Ps. fulvidraco</i>)
Unknown	Unknown	Unknown	Jiangsu	Suzhou	Wang (1964)
			—	—	—
			—	—	—

* Kuang and Qian (1991) stated that *A. coregoni* occurs in Hebei Province, Inner Mongolia, the Yangtze River basin, and southern and southwestern China, but did not show any data on collection localities of each infected fish.

** Song and Kuang (1980) mentioned that *A. coregoni* is widely distributed in southern and northern China.

*** Both Chen (1973) and Wade et al. (2008) did not report on collection localities of infected fish.

Table 3. Hosts of *Argulus coregoni* reported in Malaysia. The classification scheme and scientific names of fishes are adopted from Froese and Pauly (2023). Fishes are alphabetically arranged in each family.

Host			Locality		Reference
Order	Family	Species	Province	Site	
Cypriniformes	Xenocyprididae	<i>Ctenopharyngodon idella</i>	Malacca	Freshwater Fisheries Research Station	Seng (1986) (as <i>Ct. idellus</i>)
		<i>Hypophthalmichthys nobilis</i>	Perak	Fish supplier	Seng (1986) (as big head carp)
			Jitra	Fisheries Station	Seng (1986) (as big head carp)
	Leptobarbidae	<i>Leptobarbus hoevenii</i>	Penang	Aquarium shop*	Seng (1986)
Cichliformes	Cichlidae	<i>Oreochromis</i> sp.	Selangor	Restaurant	Everts and Avenant-Oldewage (2009)

* The fish examined by Seng (1986) were introduced from Indonesia.

Table 4. Hosts of *Argulus coregoni* reported in Japan. The scientific names of fishes follow Motomura (2023), and the orders and families, to which fishes belong, are based on Froese and Pauly (2023). Fishes are alphabetically arranged in each family, and prefectures are arranged from the northeast to the southwest in the Japanese Archipelago.

Host			Locality		Reference
Order	Family	Species	Prefecture	Site	
Salmoniformes	Salmonidae	<i>Oncorhynchus masou ishikawae</i>	Gifu	Gero Branch, Gifu Prefectural Research Institute for Fisheries and Aquatic Environments	Hosoe et al. (1975) (as <i>On. rhodurus</i>), Tokuhara et al. (2010, 2019), Tokuhara (2019), Nagasawa et al. (2020a)
				Maze River	Nagasawa et al. (2022b)
				Hida River	Nagasawa et al. (2022b)
				Yoshida River	Nagasawa et al. (2022b)
			Shiga	Lake Biwa basin	Grygier (2004)
				Echi River	Nagasawa and Kawai (2019)
				Kawachidani Stream (Ishida River)	Nagasawa (2009, 2023c)
				Oike River	Nagasawa (2009, 2023c)
			Nara	Kanzaki River	Nagasawa (2009, 2023c)
				Kawarabi River	Tamura and Maruyama (2009), Tamura (2009)
			Wakayama	Hiki River	Takegami (1984) [as <i>Salmo</i> (<i>On.</i>) <i>mas. macrostomus</i>]
				Fisheries Laboratory	Nagasawa and Ohya (1996a) (as <i>On. mas. ishikawai</i>), Kaji et al. (2011) (as <i>On. mas. ishikawai</i>)
			Hyogo	Institute of Hanzaki	Nagasawa et al. (2009)
			Shimane	San-no-tani Stream	Nagasawa and Kawai (2016)
			Hiroshima	Nakatsudani River	Nagasawa et al. (2009)
			Yamaguchi	Usa River	Nagasawa et al. (2017)
				Negasa River	Nagasawa et al. (2017)
				Shimaji River	Nagasawa et al. (2017)
				Trout farm	Nagasawa et al. (2017)
			Tokushima	Trout farm	Yuasa (2014), Nagasawa and Yuasa (2020)
		<i>Oncorhynchus mas. masou</i>	Akita	Ani River	Nagasawa et al. (2020b)
				Trout farm	Nagasawa et al. (2020b)
				Busha Stream	Nagasawa and Sato (2023)
			Tokyo	Okutama Branch, Tokyo Metropolitan Fisheries Experimental Station	Inoue et al. (1980) (as <i>On. masou</i>), Shimura and Egusa (1980) (as <i>On. masou</i>), Shimura (1981, 1983a, b) (as <i>On. masou</i>), Shimura et al. (1983a, b) (as <i>On. masou</i>), Shimura and Inoue (1984) (as <i>On. masou</i>)
				Asakawa River	Nagasawa (2017b)
			Aichi	Horai Fish Farm	Uno et al. (1975), Ishii et al. (1978)
			Gifu	Itoshiro River	Nagasawa et al. (2022b)
			Ishikawa	Fisheries Research Center	Nagasawa and Ishiyama (2019)
			Fukui	Mountain stream	Kato (1964)
			Shimane	San-no-tani Stream	Nagasawa and Kawai (2016)
			Kumamoto	Nakabaru River	Nagasawa et al. (2019a)
		<i>Oncorhynchus mykiss</i>	Tochigi	Fishing ponds	Nagasawa et al. (2015)
				Fish farm	Nagasawa et al. (2015)
			Tokyo	Yoshino Fish Farm, Tokyo Fisheries Research Institute	Hoshina (1950) (as <i>Salmo irideus</i>)
				Okutama Branch, Tokyo Metropolitan Fisheries Experimental Station	Shimura and Egusa (1980) (as <i>Salm. gairdneri</i>), Shimura (1983a) (as <i>Salm. gairdneri</i>), Shimura et al. (1983b) (as <i>Salm. gairdneri</i>), Shimura and Inoue (1984) (<i>Salm. gairdneri</i>)
			Nagano	Kizaki Branch, National Fisheries Research Institute	Hoshina (1950) (as <i>Salm. irideus</i>)
			Gifu	Gero Branch, Gifu Prefectural Research Institute for Fisheries and Aquatic Environments	Hosoe et al. (1975) (<i>Salm. gairdneri</i>)
			Aichi	Horai Fish Farm	Uno et al. (1975), Ishii et al. (1978)
			Wakayama	Fish farm	Hoshina (1950) (as <i>Salm. irideus</i>)
			Tochigi	Lake Chuzeji	Nagasawa (2009)
		<i>Salmo trutta</i>	Tochigi	Lake Chuzeji	Nagasawa (2009)

Table 4. Continued.

Host			Locality		Reference
Order	Family	Species	Prefecture	Site	
Salmoniformes	Salmonidae	<i>Salvelinus fontinalis</i>	Tochigi	Fish farm	Nagasawa et al. (2015)
			Tokyo	Yoshino Fish Farm, Tokyo Fisheries Research Institute	Hoshina (1950)
				Okutama Branch, Tokyo Metropolitan Fisheries Experimental Station	Inoue et al. (1980), Shimura and Egusa (1980)
			Nagano	Akashina Fisheries Guidance Center	Hoshina (1950)
		<i>Salvelinus leucomaenis imbrius</i>	Shimane	Takatsu River	Nagasawa and Kawai (2008)
		<i>Salvelinus l. japonicus</i>	Nagano	Kesa-zawa Stream	Nagasawa and Kawai (2015)
			Gifu	Maze River	Nagasawa et al. (2021b, 2022b) (as <i>Salv. leucomaenis</i>)
				Hida River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
				Tsukechi River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
				Itoshiro River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
				Sho River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
				Gamada River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
			Aichi	Horai Fish Farm	Ishii et al. (1978)
		<i>Salvelinus l. leucomaenis</i>	Akita	Ani River	Nagasawa et al. (2020b)
		Hybrid (<i>Salv. l. leucomaenis</i> × <i>On. mas. masou</i>)	Gifu	Itoshiro River	Nagasawa et al. (2022b) (as <i>Salv. leucomaenis</i>)
		Unspecified salmonid	Aichi	Horai Fish Farm	Ishii (1979)
Plecoglossidae	<i>Plecoglossus altivelis altivelis</i>		Akita	Ani River	Nagasawa et al. (2019b, 2020b)
				Nukazawa River	Nagasawa and Sato (2023)
			Tochigi	Mumo River	Nagasawa et al. (2015)
				Naka River	Nagasawa et al. (2015)
			Nagano	Akashina Fisheries Guidance Center	Hoshina (1950) (as <i>Pl. altivelis</i>)
			Gifu	Nagara River	Nagasawa et al. (2018b, 2020c), Nagasawa and Morikawa (2019a)
				Maze River	Nagasawa et al. (2018b)
				Shira River	Nagasawa et al. (2018b)
			Aichi	Toyo River	Nagasawa et al. (2018b), Nagasawa and Morikawa (2022a)
			Fukui	Asuwa River	Nagasawa and Morikawa (2022b)
			Shiga	Ado River	Nagasawa et al. (2018b)
			Mie	Miya River	Nagasawa et al. (2018b)
				Ouchiyama River	Nagasawa and Morikawa (2019b) (= Ōuchiyama River), Katahira et al. (2021)
			Kyoto	Hozu River	Yamaguti (1937)*
			Wakayama	Fisheries Laboratory	Nagasawa and Ohya (1996b) (as <i>Pl. altivelis</i>)
			Shimane	Takatsu River	Nagasawa and Morikawa (2019c)
			Kochi	Doi River	Nagasawa and Ikeda (2011)
Cypriniformes	Acheilognathidae	<i>Acheilognathus</i> sp.	Shiga	Otsu	Tokioka (1936) (as <i>Ac. moriokae</i>)
		<i>Tanakia limbata</i>	Okayama	Asahi River	Nagasawa and Taniguchi (2021)
	Xenocypridae	<i>Nipponocypris temminckii</i>	Wakayama	Takase River	This study
Siluriformes	Amblycipitidae	<i>Liobagrus reinii</i>	Fukushima	Aga River	Nagasawa and Ishikawa (2015)
Gobiiformes	Odontobutidae	<i>Odontobutis hikimius</i>	Shimane	Ishitani River	Nagasawa et al. (2014)
Unknown	Unknown	Unknown	Miyagi	Naruse River	Nagasawa et al. (2023c)
			Gifu	Nagara River	Nagasawa (2023d)
			Shiga	Harihata River	Nagasawa (2009, 2023c)
				Ane River	Nagasawa (2009, 2023c)
			Kyoto	Chimidani River	Nagasawa et al. (2013)
			Nara	Higashino River (Kami-kitayama)	Nagasawa and Ohya (1996a: 87, footnote), Nagasawa (2009)

* Yamaguti (1937) described *A. plecoglossi* Yamaguti, 1937, but it has been regarded as a junior synonym of *A. coregoni*.

Takase River), where the following six species of freshwater fishes are also found: ayu, Japanese eel *Anguilla japonica* Temminck and Schlegel, 1846 (Anguilliformes: Anguillidae), and four species of the gobiiform Gobiidae [dusky floating goby *Gymnogobius petschiliensis* (Rendahl, 1924); yoshinobori goby (cross band type) *Rhinogobius nagoyae* Jordan and Seale, 1906; short-spined Japanese trident goby *Tridentigobius brevispinis* Katsuyama, Arai and Nakamura, 1972; and parrot goby *Sicyopterus japonicus* (Tanaka, 1909)] (R. Uchiyama, unpublished data). Of these species, dark chub was predominant and other fishes were in very low abundance, but it is necessary to examine the occurrence of *A. coregoni* on these sympatric fishes for evaluating the importance of dark chub as the host.

As mentioned above, *A. coregoni* has been reported from salmonids and ayu in the upper and middle-lower reaches of rivers, respectively, in the two prefectures, central Japan, and *A. coregoni*-infected salmonids and ayu were collected at elevations of 237–873 m and 65–557 m, respectively, in Gifu Prefecture, and those fishes were also caught at elevations of ca. 380–650 m and 92 m, respectively, in Shiga Prefecture (Nagasawa et al. 2022b; Nagasawa 2023c). In addition, Nagasawa and Kawai (2015) reported that a Japanese char *Salvelinus leucomaenis japonicus* Oshima, 1961 was infected with *A. coregoni* at 1075 m elevation in a mountain stream in Nagano Prefecture, central Japan. In comparison with these elevation data, the specimen of *A. coregoni* reported in this paper was collected at an extremely low-elevation (15 m). Moreover, Nagasawa and Taniguchi (2021) did not record the elevation at which *A. coregoni* parasitized an oily bitterling in the lower reaches of the Asahi River, Okayama Prefecture, but it is here found that these authors also collected the infected fish at 15 m elevation. In central Japan, *A. coregoni* and *A. japonicus* have their own habitat preference dependent on different environmental conditions: *A. coregoni* occurs in the running waters, especially in the colder, well oxygenated mountain streams, while *A. japonicus* inhabits the still or slow-flowing waters (Nagasawa 2023c). The investigated Takase River is a small stream and has very clear running waters and, from these facts, we infer that this river provides *A. coregoni* with a suitable habitat. In other words, we suggest that, in central Japan, *A. coregoni* maintains its population even in extremely low-elevation streams under suitable running-water conditions as well as in high-elevation mountain streams.

Based on literature published between 1936 and 2023, information on the hosts and collection localities of *A. coregoni* in East Asia is tabulated (Tables 1–4). To date, 12 species (in eight families and five orders), nine species (in six families and four orders), and four species (in three families and two orders) of fishes have recorded as hosts of *A. coregoni* from the Russian Far East (Table 1), China (Table 2), and Malaysia (Table 3), respectively. In Japan, this parasite is known to infect 11 species and three subspecies (in six families and four orders) of fishes (Table 4). There is no record of *A. coregoni* from other countries of East Asia. Thus, a total of 31 species and three subspecies of freshwater fishes have so far been reported as hosts of *A. coregoni*

in East Asia, and these fishes belong to 16 families and eight orders. This indicates that *A. coregoni* is not a host-specific parasite. Moreover, it is interesting to note that, excluding four species [common carp *Cy. carpio*; grass carp *Ctenopharyngodon idella* (Valenciennes, 1844); Amur catfish *Silurus asotus* Linnaeus, 1758; and yellow catfish *Tachysurus fulvidraco* (Richardson, 1846)], the remaining 27 species and three subspecies of host fishes have been recorded from a single country, which suggests that *A. coregoni* utilizes fishes occurring in individual countries as its hosts. In addition, this parasite is widely distributed in the subarctic (the Russian Far East), temperate (China and Japan), and subtropical (Malaysia) regions, and its habitat is very likely to differ between the three regions, especially the subarctic and subtropical regions. In Japan, *A. coregoni* occurs in well oxygenated, running waters (Nagasawa 2023c) and frequently infects salmoniform fishes (Table 4), and a similar habitat and host utilization has been reported for this species in the temperate and subarctic regions of Europe (Campbell 1971; Mikheev et al. 2015). Contrary to this, in China and Malaysia, for example, grass carp (Xenocyprididae) is one of the known hosts of *A. coregoni* (Tables 2, 3) and this fish inhabits large, slow-flowing or standing water bodies, such as lakes, ponds, pools, and backwaters of large rivers (Froese and Pauly 2023), which implies that *A. coregoni* has adapted to such lentic water conditions and can infect non-salmoniform fishes in these countries. As discussed in the above Remarks, *A. coregoni* from China and Malaysia is morphologically identical to the species from Japan and European countries, but no genetic population study has yet been conducted for *A. coregoni*. It is thus desirable to conduct a molecular analysis of the populations of this species from various locations in East Asia and other distribution areas in order to clarify its genetic diversity.

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Authors Contributions

Kazuya Nagasawa: Conceptualization; Resources; Formal Analysis; Visualization; Writing – original draft; Writing – review & editing. Ryu Uchiyama: Investigation; Visualization; Writing – review & editing. Ko Tomikawa: Supervision; Writing – review & editing.

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Declarations

Competing interests. The authors declare no conflicts of interest.

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