Doctor Thesis

Taxonomic studies on monogeneans parasitic on cyprinids and alien freshwater fishes in Japan

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Contents

Chapter 1. Introduction

The class Monogenea van Beneden, 1858 (Platyhelminthes) is commonly parasitic on or in aquatic or amphibious vertebrates, mainly fishes, but rarely on aquatic invertebrates (Yamaguti 1963). The vast majority of monogeneans have simple, direct life cycles, i.e. without using intermediate hosts. Most species show strict specificity for their hosts. Monogeneans, excluding the viviparous family Gyrodactylidae Cobbold, 1864, produce eggs, and a larva called oncomiracidium hatches. Their posterior organs are used to attach to a host, and the blood or epithelial cells of the host are fed on. Attachment and feeding by a large number of monogeneans can induce diseases and mortalities of fishes in aquaculture systems as well as in natural waters such as lakes, rivers, and seas (Yamaguti 1963; Hayward 2005; Whittington 2005; Buchmann and Bresciani 2006).

About 3,000 species of monogeneans have so far been described in the world. However, considering their strict host specificity, each fish species may be parasitized by at least a single species of monogenean. If this prediction is correct, there may be about 25,000 species of monogeneans, equivalent to the total number of fishes in the world (Whittington 1998). In total, 4,370 species of fishes are known to occur in Japan (Nakabo 2013; Anonymous 2016), where 228 species of monogeneans have been reported from only 170 species of fishes, 3 species of reptiles, 9 species of amphibians, and 3 species of invertebrates (Table 1). Of these monogeneans, 76 nominal species have been reported from freshwater fishes, and most of these fishes are commercially important species, such as common carp *Cyprinus carpio* Linnaeus, 1758, crucian carps *Carassius* spp. (Cyprinidae), Japanese weatherfish *Misgurnus anguillicaudatus* (Cantor, 1842) (Cobitidae), eels *Anguilla* spp. (Anguillidae), ayu *Plecoglossus altivelis altivelis* (Temminck and Schlegel, 1846) (Plecoglossidae), and various species of Salmonidae (Table 1). Thus, much remains to be studied on the monogenean fauna of wild Japanese freshwater fishes. In addition, a number of freshwater fishes occur as endemic in Japan (Hosoya 2015b), and endemic monogeneans also may exist. A total of 167 species of freshwater fishes are listed in the Red Data Book of Japan (Hosoya 2015a), extinction and sudden decrease of wild hosts and alteration of local ecosystems have been suggested to cause co-extinction of their parasites (Windsor 1990; Stork 1993; Baruš *et al*. 1997, Urabe 2010), and host-specific monogeneans may be under the same situation. Many domestic fishes also have been stocked into many sites of Japan and affected the Japanese endemic species, which has caused the verge of extinction of the latter animals (Matsuzawa and Senou 2008). Thus, it is important and necessary to understand the monogenean fauna of Japanese freshwater fishes in terms of conservation of biodiversity.

Moreover, the monogeneans can establish more readily together with their hosts than other groups of parasites because of their simple life cycle (Bauer and Hoffman 1976), and some of alien monogeneans have caused negative impacts for wild fish stocks (*e.g.* Petrushevski and Shulman 1970; Johnsen and Jensen 1986; Ogawa 2002; Yoshinaga *et al*. 2009). It is necessary to clarify the monogenean fauna of alien fishes introduced from other countries into Japan.

This thesis deals with taxonomy of monogeneans from Japanese cyprinids and alien freshwater fishes collected in central Honshū to the Ryūkyū Islands, Japan. It consists of five chapters. Following two chapters (Chapter 1 herein as Introduction, and Chapter 2 as Materials and Methods), there are three chapters (Chapters 3, 4, and 5) with Acknowledgments and References. In Chapters 3 and 4, I describe four and six species of monogeneans from cyprinids and alien fishes in Japan, respectively, based on my published papers (Nitta and Nagasawa 2013, 2014b, c, 2015b, 2016a, b, c). Finally, I discuss my findings in Chapter 5.

Chapter 2. Materials and Methods

Fishes were collected from waters of Japan from 2012 to 2015 using various methods, such as hand net, cast net, trap net, and angling. Sampling locations are listed in Table 2. Since two sampling sites in Tokushima Prefecture were located near the sea, the water collected at the sites was measured for salinity using a calibrated hydrometer (Instant Ocean TK504, USA). Fishes were brought on ice or alive to the laboratories at Hiroshima University, Higashi-Hiroshima city, Hiroshima Prefecture or University of the Ryukyus (University Museum [Fujukan], Nishihara town; and Tropical Biosphere Research Center, Iriomote Station, Taketomi town), Okinawa Prefecture and examined for helminth parasites under a dissecting microscope.

Monogeneans were picked up from the gills using small needles and forceps, and flattened under coverslip pressure. Some specimens were identified under slight coverslip pressure and preserved in 99% ethanol for molecular analysis. Other specimens were fixed in 70% ethanol or acetic-acid–formalin–alcohol (AFA) and stained in Heidenhain's iron hematoxylin, alum carmine or Gomori's trichrome, while some were fixed in ammonium picrate glycerin (APG) (Lim 1991). All specimens except the ones reserved for molecular study were dehydrated through a graded ethanol series, cleared in xylene, and mounted in Canada balsam. Drawings were made with the aid of a drawing tube attached to an Olympus BX51 light microscope. Axes of measurement of sclerotized parts of *Dactylogyrus* Diesing, 1850 and *Ancyrocephalus* Creplin, 1839, those of *Ligictaluridus* Beverley-Burton, 1984 and *Salsuginus* Beverley-Burton, 1984, and those of monogeneans parasitic on *Pterygoplichthys disjunctivus* (Weber, 1991) are presented in Figs. 1, 2, and 3, respectively. The measurements and terminology of *L. pricei* (Mueller, 1936) and *S. seculus* (Mizelle and Arcadi 1945) follow Klassen and Beverley-Burton (1985a, b) and Murith and Beverley-Burton (1985), respectively, and the method to measure sclerotized structures of *Unilatus* Mizelle and Kritsky, 1967 and *Trinigyrus* Hanek, Molnar, and Fernando, 1974 is modelled on Mizelle and Klucka (1953), Kritsky *et al*. (1986), and Branches and Domingues (2014). Some measurements were obtained on images taken by an Olympus DP20 using ImageJ software (version 1.48i). Measurements, in micrometers, are expressed as the mean±standard deviation followed in parentheses by the range and the number (*n*) of specimens examined. The numbering of marginal hook pairs follows Mizelle (1936) and Llewellyn (1963) for *Unilatus* and the others, respectively. The direction of coiling of the penis is as determined in ventral view (Kritsky *et al*. 1985). Dactylogyridae sensu Boeger and Kritsky (1993) is accepted in this thesis except that in Table 1. Prevalence and intensity of infection are as defined by Bush *et al*. (1997). All fishes were identified based on Nakabo (2013), and the scientific and common names of fishes used in this thesis follow Froese and Pauly (2016) except for the Kazetoge bittering, *Rhodeus atremius atremius* (Jordan and Thompson, 1914) (Kawamura 2015a) and common names of Japanese freshwater fishes (Hosoya 2015b). All specimens described herein are deposited in the Platyhelminthes collection of the National Museum of Nature and Science, Tsukuba city, Ibaraki Prefecture (NSMT-Pl) and the University Museum, University of the Ryukyus (Fujukan, RUMF), Nishihara town, Okinawa Prefecture, Ryūkyū, Japan.

DNA was extracted from one specimen each of *Dactylogyrus bicorniculus* Nitta and Nagasawa, 2016, *Unilatus unilatus* Mizelle and Kritsky, 1967 and *Trinigyrus peregrinus* Nitta and Nagasawa, 2016 using the DNeasy blood and tissue kit (Qiagen) in accordance with the manufacturer's instructions. Partial fragment of the 28S rDNA was amplified by polymerase chain reaction (PCR) using the primer pairs C1 (5′-ACCCGCTGAATTTAAGCAT-3′) and D2 (5′-TGGTCCGTGTTTCAAGAC-3′) for *D. bicorniculus*, and Ancy55F (5′-GAG ATT AGC CCA TCA CCG AAG-3′) and L1200R (5′-GCA TAG TTC ACC ATC TTT CGG-3′) for *U. unilatus* and *T. peregrinus* (Hassouna *et al*. 1984; Littlewood *et al*. 2000; Plaisance *et al*. 2004). A total of 25 µL PCR reaction mixture consisted of 1 µL of DNA template, 10× Titanium Taq PCR Buffer (Clonetech), 0.2 mM of each dNTP, 1 µM of each primer, and 1× Titanium Taq DNA Polymerase (Clonetech). PCR was carried out with the following protocol: 94°C for 30 sec followed by 35 cycles of 94°C for 30 sec, 56°C for 30 sec, and 72°C for 2 min, and 10 min of final hold at 72°C. PCR products were purified using NucleoSpin Gel and PCR Clean-up kit (Macherey-Nagel) and sequenced with a 3130X Genetic Analyzer (Applied Biosystems) with the same primers that generated the PCR products. The sequences of *U. unilatus* and *T. peregrinus* were compared with GenBank entries using BLAST (http://www.ncbi.nlm.nih.gov/BLAST/) software in December, 2015. The 28S rDNA sequences of *D. bicorniculus*, 44 species of Dactylogyridae sensu Kritsky and Boeger (1989) (1 species of *Actinocleidus* Mueller, 1937; 2 species of *Ancyrocephalus* Creplin, 1839; 1 species of *Caballeria*; Bychowsky and Nagibina, 1970; 1 species of *Cleidodiscus* Mueller, 1934; 17 species of *Dactylogyrus* Diesing, 1850; 1 species of *Ergenstrema* Paperna, 1964; 5 species of *Euryhaliotrema* Kritsky and Boeger, 2002; 5 species of *Haliotrema* Johnston and Tiegs, 1922; 3 species of *Ligophorus* Euzet and Suriano, 1977; 1 species of *Metahaliotrema* Yamaguti, 1953; 2 species of *Protogyrodactylus* Johnston and Tiegs, 1922; 2 species of *Pseudodactylogyrus* Gussev, 1965; 1 species of *Pseudohaliotrema* Yamaguti, 1953; 1 species of *Thaparocleidus* Jain, 1952; 1 species of *Urocleidus* Mueller, 1934), and as outgroups, each one species of *Anoplodiscus* Sonsino, 1890 (Anoplodiscidae) and *Pseudomurraytrema* Bychowsky, 1957 (Pseudomurraytrematidae) downloaded from GenBank (accession numbers written in Fig. 8), were edited and aligned with ClustalW using the default parameter, verified/edited visually, and phylogenic trees were constructed for neighbor-joining (NJ) and minimum evolution (ME) methods using Kimura's 2-parameter method with the phylogeny tested by 1000 bootstrap repeats using MEGA 6 (Tamura *et al*. 2013). PCR products of the 28S rDNA gene were submitted to the DDBJ (DNA Data Bank of Japan) database.

Chapter 3. Monogeneans from Cyprinids in Japan

3.1 Monogeneans of the Topmouth Gudgeons *Pseudorasbora* spp.

3.1.1 Introduction

Cyprinids of the gobionine genus *Pseudorasbora* Bleeker, 1860 are natively distributed in Far East Asia, and three species occur in Japan (Nakamura 1969; Miyadi *et al.* 1976; Nakabo 2013; Kawase and Hosoya 2015). *Pseudorasbora pumila* Miyadi, 1930 is endemic to central Honshū, Japan, and is on the verge of extinction because of competition and hybridization with introduced fishes and artificial alteration of the habitat (Nakamura 1969; Uchiyama 1989; Konishi *et al.* 2003, 2009; Konishi and Takada 2004, 2013; Konishi 2010). It has been designated as an endangered species by the Ministry of the Environment of Japan (Sugiyama 2015). On the other hand, *Pseudorasbora parva* (Temminck and Schlegel, 1846) occurs in Japan, Korea, and China (Nakabo 2013). In Japan, the latter species is popular in recreational fishing and has a wider distribution range than *P. pumila* (Nakamura 1969; Anonymous 2010a). In this section, I redescribe *Dactylogyrus squameus* Gussev, 1955 and *Ancyrocephalus pseudorasborae* Achmerow, 1952 from *P. parva* and *Bivaginogyrus obscurus* (Gussev, 1955) from *P. pumila* and *P. parva*.

3.1.2 Results

3.1.2.1 ***Dactylogyrus squameus*** Gussev, 1955

(Fig. 4)

Dactylogyrus squameus Gussev, 1955: 207–209, fig. 10-3; Bykhovskaya-Pavlovskaya *et al.* 1962: 310, 312, fig. 619; Anonymous 1978: 51; Hu and Chen 1979: 123; Chen 1981: 115; Lu and Lang 1981: 252; Zhang 1981: 71; Ji *et al.* 1982: 21; Chen 1984: 53; Gussev 1985: 133, fig. 178; Gvozdev and Agapova 1988: 109, 112; Ma and Li 1991: 7; Wu and Wang 1991: 121, fig. 120; Gibson *et al.* 1996: 30; Liang 2000: 243–244, fig. 192; Ondračkova *et al.* 2004: 140, 143–144, fig. 5; Šimkova *et al.* 2004: 1003, 1006, 1007, 1008, 1011; Šefrova and Laštůvka 2005: 157; Galli *et al.* 2007: 265, 267, 269, 270; Gerasev 2008: 407; Karabekova 2008: 331, 333; Gozlan *et al.* 2010: 330, 331; Gussev *et al.* 2010: 199, 201, fig. 229; Anonymous 2012: 51, 52; Davydov *et al.* 2012: 73, 74; Witkowski and Grabowska 2012: 81; Balbuena *et al.* 2013: 4; Ekmekci *et al.* 2013: 116; Xiao 2015: 27–28, 64–65, figs 2.14b–d, 2.15.

Neodactylogyrus squameus: Yamaguti 1963: 43, fig. 703.

Material examined. Ten specimens were used for the description: eight specimens fixed in APG (NSMT-Pl 6176, 6177); one specimen stained in Heidenhain's iron hematoxylin (NSMT-Pl 6179 together with two specimens of *B. obscurus*); and one specimen (NSMT-Pl 6178) stained in alum carmine; from Ibaraki, Nara, and Tottori prefectures, respectively.

Description. Body (Fig. 4A) length including haptor 526±133.0 (241–683, *n*=9), width at mid-body 76±15.3 (57–102, *n*=9). Three pairs of head organs. Two pairs of eye-spots. Alimentary system consisting of subspherical pharynx, length 31±5.0 (20–37, *n*=9), width 28±5.1 (20–35, *n*=9), followed by esophagus and bifurcate intestine with branches confluent just anterior to tests. Testis pyriform, dorsal to ovary. Vas deferens arising from anterior region of testis, looping around left intestine towards ventral side of body, distended as seminal vesicle before entering base of penis. Two prostatic reservoirs both saccate. Copulatory organ (Fig. 4L) consisting of penis and accessory piece. Penis a curved tube, length 22±1.2 (20–24, *n*=8), tube length 22±1.7 (19–24, *n*=8). Sclerotized accessory piece sigmoid, its root touching base of copulatory organ and holding copulatory organ by its process; accessory piece length 21±1.6 (19–24, *n*=8). Ovary in mid-body. Oviduct arising from anterior side of ovary, continuing as oötype surrounded by Mehlis' gland and uterus. Vagina unsclerotized, running ventrally from right side of seminal receptacle located to right of oötype to vaginal opening on right body surface. Vitellaria approximately co-extensive with intestine.

Haptor length 72±14.1 (43–94, *n*=9), width 106±30 (62–138, *n*=9). Dorsal anchor (Fig. 4B) of total length 33±2.4 (28–35, *n*=10), length to notch 28±1.9 (25–30, *n*=10), outer root length 5±0.5 (4–5, *n*=10), inner root length 8±1.2 (7–10, *n*=10), point length 10±0.7 (9–11, *n*=10). Dorsal bar (Fig. 4C) bow-shaped, of total length 22±1.4 (21–25, *n*=10), total width 8±0.7 (7–9, *n*=10), median width 5±0.6 (4–6, *n*=10). Ventral bar (Fig. 4D) thin, slightly curved, of total length 24±2.6 (21–28, *n*=7), total width 2±1.0 (1–4, *n*=7), median width 1.1±0.4 (1–2, *n*=7). Marginal hooks in 7 pairs; length: pair I (Fig. 4E) 17±1.0 (15–18, *n*=9); pair II (Fig. 4F) 19±1.1 (18–21, *n*=9); pair III (Fig. 4G) 22±1.0 (20–23, *n*=9); pair IV (Fig. 4H) 25±1.9 (22–27, *n*=9); pair V (Fig. 4I) 22±1.0 (21–24, *n*=9); pair VI (Fig. 4J) 21±1.0 (20–23, *n*=9); pair VII (Fig. 4K) 19±1.0 (17–20, *n*=9). Pair of needles (Fig. 4M) of length 9±0.9 (8–10, *n*=9), located near tips of second hooks.

Host. Topmouth gudgeon *Pseudorasbora parva* (Cypriniformes: Cyprinidae).

Localities. The Tomio River, Tomio-gawa-nishi, Nara city, Nara Prefecture; the Kitakata River, Kitakata, Nanbu town, Saihaku County, Tottori Prefecture; Lake

Kasumigaura, Okijuku-machi, Tsuchiura city, Ibaraki Prefecture.

Site of infection. Gill filaments.

Prevalence and intensity range (mean). 100% (2/2) and 1–2 (1.5) in the Tomio River, Nara Prefecture; 25% (1/4) and 1 in the Kitakata River, Tottori Prefecture; 40% (4/10) and 1–3 in Lake Kasumigaura, Ibaraki Prefecture.

Remarks. *Dactylogyrus squameus* was originally described by Gussev (1955) from the gills of *Pseudorasbora parva* from the Amur River and Lake Chanka, Far-East Russia, and subsequently reported from the same host in Heilongjiang, Liaoning, Hubei, and Yunnan, China (Ji *et al.* 1982; Chen 1984; Wu and Wang 1991; Liang 2000). The species was transferred to the genus *Neodactylogyrus* by Yamaguti (1963), although this genus had been synonymized with *Dactylogyrus* by Mizelle and Donahue (1944). The specimens examined in this study almost conform to the descriptions and illustrations of *D. squameus* by Gussev (1955, 1985), Bykhovskaya-Pavlovskaya *et al.* (1962), Wu and Wang (1991), Liang (2000), Ondračkova *et al.* (2004), and Gussev *et al.* (2010). The dorsal anchors of my specimens are slightly smaller than those authors' measurements, but this may be due to intraspecific variation because the anchor's shape and the male copulatory organs of my specimens agree with the cited descriptions. This monogenean established populations infecting *Pseudorasbora parva* in Kazakhstan, Tajikistan, the Kyrgyz Republic, Ukraine, the Czech Republic, Slovak Republic, and Italy after both species were introduced from China and/or Far-East Russia into these countries (Gussev 1985; Gvozdev and Agapova 1988; Ondračkova *et al.* 2004; Galli *et al.* 2007). Ondračkova *et al.* (2004) listed the monogenean as occurring in "Uzbekistan" by reference to Gussev (1985), but this was most probably a mistranslation of "Ukraine".

3.1.2.2 ***Bivaginogyrus obscurus*** (Gussev, 1955)
(Fig. 5)

Dactylogyrus obscurus Gussev, 1955: 206–207, figs 10.1, 10.2; Bykhovskaya-Pavlovskaya *et al.* 1962: 307, fig. 613; Strelkov 1971: 53; Anonymous 1973: 140, figs 163–164; Anonymous 1978: 45; Hu and Chen 1979: 123; Chen 1981: 115; Lu and Lang 1981: 252; Huang 1986: 16; Gvozdev and Agapova 1988: 109, 112; Davydov *et al*. 2012: 74.

Neodactylogyrus obscurus: Yamaguti 1963: 41, fig. 623.

Bivaginogyrus obscurus: Gussev and Gerasev 1985: 192–194, figs 289, 291; Gussev and Gerasev 1986: 373–375, fig. 1; Ma and Li 1991: 9; Wu and Wang 1991: 133–135, figs 139–140; Matsaberidze 1993: 9; Zhao and Ma 1995: 15; Xia *et al.* 1999: 59;

Zhang *et al*. 1999: 130–131, fig. 8-13; Wu 2000b: 426–428, fig. 378; Karabekova 2008: 331; Gerasev 2008: 407, 411, 419; Gussev *et al.* 2010: 274–275, figs 345–346; Anonymous 2012: 51–52; Davydov *et al.* 2012: 73; Teo *et al.* 2013: 3–8, figs 1A, 2, 3, 4, 8A, 8B.

Material examined. Fifteen specimens (NSMT-Pl 6131) and one specimen (NSMT-Pl 6132) from *P. pumila* collected on 23 July and 30 October 2013, respectively; and 14 specimens (NSMT-Pl 6133) and five specimens (NSMT-Pl 6134) from *P. parva* collected on 13 and 16 June 2014, respectively.

Additional specimens. Two and three specimens collected from the Tomio River, Nara Prefecture (NSMT-Pl 6179), and the Senō River, Okayama Prefecture (NSMT-Pl 6182), respectively.

Description. Body (Fig. 5A) including haptor length 301±55.3 (128–411; *n*=34), width at mid-body 43±9.3 (24–68; *n*=34). Surface of body corrugated. Three pairs of head organs. Two pairs of eye-spots with some accessory eyes. Pharynx spherical, diameter 16±3.7 (11–28; *n*=33); short esophagus followed by bifurcate intestine with branches confluent posterior to testis. Testis ovate to pyriform, postero-dorsal to ovary. Vas deferens leaving from anterior margin of testis, looping dorsoventrally around left intestine, and distending small seminal vesicle before entering into base of penis. Two prostatic reservoirs both saccate. Male copulatory organ (Fig. 5M, N) consisting of penis and accessory piece. Penis a curved tube, length 18±1.7 (16–21; *n*=30). Sclerotized accessory piece (Fig. 5M, N) touching base of penis, extending along penis, and covering point of penis in spatulate distal expansion, latter with process attaching to inner tip; length of accessory piece 14±1.5 (10–16; *n*=34). Ovary in mid-body. Two vaginal pores (Fig. 5O) opening individually on both sides of mid-body surface, two vaginae each connecting oötype. Oötype surrounded by Mehlis' gland. Oviduct arising from anterior margin of ovary, continues as oötype. Vitellaria approximately co-extensive with intestine.

Haptor length 42±9.3 (28–70; *n*=34), width 118±32.1 (49–192; *n*=33). Dorsal anchor (Fig. 5B) lacking outer root, total length 25±2.3 (21–29; *n*=33), shaft length 20±1.7 (18–24; *n*=33), root length 7±1.5 (3–9; *n*=33), point length 11±1.2 (9–13; *n*=34). Dorsal bar (fig. 5C) total length 26±2.4 (21–30; *n*=34), total width 5±1.1 (3–8; *n*=34), median width 2±0.3 (1–3; *n*=34). Ventral bar (Fig. 5D) W-shaped, total length 45±3.5 (37–52; *n*=32), total width 6±1.8 (3–11; *n*=30), median width 1±0.3 (1–2; *n*=32). Hooks in 7 pairs; hook length: pair I (Fig. 5E) 14±0.7 (13–15; *n*=34); pair II (Fig. 5F) 16±1.0 (14–18; *n*=34); pair III (Fig. 5G) 17±1.0 (15–18; *n*=34); pair IV (Fig. 5H) 16±0.9 (14–18; *n*=32); pair V (Fig.

5I) 23±1.0 (21–25; *n*=34), pair VI (Fig. 5J) 24±1.4 (21–27; *n*=34); pair VII (Fig. 5K) 17±0.8 (15–18; *n*=34). Pair of needles present (Fig. 5L), length 7±0.6 (6–8; *n*=25), located near second hooks.

Hosts. Shinai topmouth gudgeon *Pseudorasbora pumila*; topmouth gudgeon *P. parva* (Cypriniformes: Cyprinidae)

Localities. Ponds of Utabi and Yamabuse, Shinonoi, Nagano city, Nagano Prefecture (*P. pumila*); Lake Kasumigaura, Okijuku-machi, Tsuchiura city, Ibaraki Prefecture (*P. parva*); the Tomio River, Tomio-gawa-nishi, Nara city, Nara Prefecture (*P. parva*); the Senō River, Uchio, Minami Ward, Okayama city, Okayama Prefecture, Okayama Prefecture (*P. parva*).

Site of infection. Gill filaments.

Prevalence and intensity range (mean). 100% (11/11) of *P. pumila* with no data for intensity in Utabi and Yamabuse, Nagano Prefecture. 80% (8/10) of *P. parva* and 1–8 (5.4) worms in Lake Kasumigaura, Ibaraki Prefecture; 50% (1/2) and 2 in the Tomio River, Nara Prefecture; four worms infected one *P. parva* in the Senō River, Okayama Prefecture.

Remarks. *Bivaginogyrus obscurus* was originally described by Gussev (1955) as a species of the genus *Dactylogyrus* Diesing, 1850 from *P. parva* in the Amur River Basin. Yamaguti (1963) transferred the species to the genus *Neodactylogyrus* Price, 1938, although the latter genus had been synonymized with *Dactylogyrus* by Mizelle and Donahue (1944). Subsequently, Gussev and Gerasev (1985) established a monotypic genus for the species, *Bivaginogyrus* Gussev and Gerasev, 1985, because it has a distinctive feature, two vaginae. The morphology and measurements of the species reported herein are approximately compatible with the past descriptions from Russia by Gussev (1955), Bykhovskaya-Pavlovskaya *et al.* (1962), Gussev and Gerasev (1985, 1986), and Gussev *et al.* (2010), and from China by Anonymous (1973), Wu and Wang (1991), and Wu (2000b). There is no marked difference in morphology and measurements of *B. obscurus* from *P. parva* and *P. pumila* in Japan (Fig. 5M, N; Table 3).

The parasite fauna of *P. pumila* is very poorly known. Only one parasite, *Lernaea cyprinacea* Linnaeus, 1758 (Crustacea: Copepoda) has been reported until now from a wild population of *P. pumila* (Nakamura 1963), and the plerocercoid *Gangesia parasiluri* Yamaguti, 1934 (Cestoda: Proteocephalidae) is known to infect it under experimental condition (Shimazu 1999). *Bivaginogyrus obscurus* is first helminth and the second parasite discovered from wild *P. pumila*. This monogenean is native to Far East Russia, China, and Japan (*e.g.* Wu *et al.* 2000; Gussev *et al.* 2010; this section), but it has recently been spread into the following four countries along with introduced of *P. parva* from

China and/or Far-East Russia: Georgia (Matsaberidze 1993), Kyrgyzstan (Karabekova 2008), Kazakhstan (Gvozdev and Agapova 1988), and Italy (Anonymous 2012).

The year in which *Bivaginogyrus* Gussev and Gerasev, 1985 was erected has been reported erroneously as 1986 by Gibson *et al.* (1996), Timofeeva *et al.* (1997), Gerasev (2008, 2009), and Gussev *et al.* (2010). It was, in fact, established in 1985 (Gussev and Gerasev 1985).

3.1.2.3 ***Ancyrocephalus pseudorasborae*** Achmerow, 1952

(Fig. 6)

Ancyrocephalus pseudorasborae Achmerow, 1952: 189, 194, fig. 4z; Gussev 1955: 299–300, fig. 48; Bykhovskaya-Pavlovskaya *et al.* 1962: 390, 391, fig. 742; Yamaguti 1963: 51, fig. 715; Anonymous 1973: 149, 266, figs 209–210; Anonymous 1978: 30–31; Hu and Chen 1979: 123; Zhang and Ji 1979: 212; Chen 1981: 117; Lu and Lang 1981: 252; Ji *et al.* 1982: 5; Chen 1984: 54; Gussev 1985: 203, fig. 306; Ma and Li 1991: 10; Wu 1991: 143–144, fig. 150; Zhao and Ma 1995: 15; Wu 2000c: 457–458, fig. 404; Gerasev 2008: 408, 411, 423, 424; Gussev *et al.* 2010: 286, 288, fig. 362. Davydov *et al.* 2012: 73, 74.

Material examined. Twenty specimens were used for the description. Soft anatomy was observed in 10 specimens (NSMT-Pl 6180) from Ibaraki Prefecture stained in Heidenhain's iron hematoxylin. Sclerotized structures were measured in eight and two specimens (NSMT-Pl 6180 and 6182) fixed in APG, from Ibaraki and Okayama prefectures, respectively.

Description. Body (Fig. 6A) elongate, length 400±43.6 (335–483, *n*=10) including haptor, width at mid-body 71±11.7 (55–94, *n*=10). Three pairs of head organs. Two pairs of eye-spots. Pharynx subspherical, length 26±2.0 (23–30, *n*=10), width 23±2.1 (19–26, *n*=10); esophagus present; intestine bifurcate with branches confluent just posterior to testis. Testis pyriform, dorsal to ovary. Vas deferens leaving from anterior region of testis, passing along dorsal to loop of sinistral intestine to ventral side, ascending to anterior part of copulatory organ, looping downwards and becoming distended to form seminal vesicle, narrowing to enter initial part of penis. Single prostatic reservoir elongate; prostatic gland occupying dorsal region of anterior trunk, with its duct leading into anterior part of prostatic reservoir. Copulatory organ (Fig. 6G) consisting of penis and accessory piece. Penis a slender curved tube, organ length 28±1.6 (25–30, *n*=10), tube length 50±4.0 (41–55, *n*=10); accessory piece curved in same direction as copulatory organ, trifurcate at tip, length 20±1.4 (18–22, *n*=10). Ovary ovate, in mid-body. Oviduct arising from anterior side of ovary, continuing as oötype surrounded by Mehlis' gland and uterus. Seminal receptacle dorsal to oviduct. Vagina (Fig. 6H) sclerotized, being slightly curved tube, length 17±3.1 (13–21, *n*=10), arising from anterior part of seminal receptacle and opening at midlength on right ventral body surface. Vitellaria approximately coextensive with intestine.

Haptor length 55±5.7 (44–61, *n*=10), width 74±11.2 (59–99, *n*=10). Dorsal anchor (Fig. 6B) more slender than ventral anchor, of total length 24±0.6 (23–25, *n*=10), length to notch 20±0.8 (19–21, *n*=10), outer root length 1±0.7 (0–2, *n*=10), inner root length 7±0.7 (6–8, *n*=10), point length 4±0.5 (4–5, *n*=10). Ventral anchor (Fig. 6C) of total length 20±1.2 (19–22, *n*=10), length to notch 18±0.8 (16–19, *n*=10), outer root length 1±0.5 (1–2, *n*=10), inner root length 8±1.1 (7–10, *n*=10), point length 4±0.7 (3–5, *n*=10). Dorsal bar (Fig. 6D) rod-shaped, of total length 18±0.7 (17–19, *n*=10), total width 4±0.4 (3–4, *n*=10), median width 3±0.4 (2–3, *n*=10). Ventral bar (Fig. 6E) V-shaped with posteriorly directed enlargement at each end, of total length 25±0.8 (23–26, *n*=10), total width 5±0.6 (4–6, *n*=10), median width 3±0.5 (2–4, *n*=10). Seven pairs of marginal hooks (Fig. 6F), all of approximately same length, 12±0.5 (11–12, *n*=10).

Host. Topmouth gudgeon *Pseudorasbora parva* (Cypriniformes: Cyprinidae).

Localities. Lake Kasumigaura, Okijuku-machi, Tsuchiura city, Ibaraki Prefecture; the Senō River, Uchio, Minami Ward, Okayama city, Okayama Prefecture.

Site of infection. Gill filaments.

Prevalence and intensity range (mean). 90% (9/10) with no data for intensity in Lake Kasumigaura, Ibaraki Prefecture; seven worms infected one *P. parva* in the Senō River, Okayama Prefecture.

Remarks. *Ancyrocephalus pseudorasborae* was originally described by Achmerow (1952) from the gills of *Pseudorasbora parva* in Lake Bolon, Far-East Russia. It was subsequently reported from the same host in Heilongjiang, Liaoning, Shandong, Shanghai, Jiangxi, Hubei, Zhejiang and Yunnan, China (Anonymous 1973; Ji *et al.* 1982; Chen 1984; Wu 1991, 2000b) and the Amur River, Russia (Gussev 1955, 1985; Bykhovskaya-Pavlovskaya *et al.* 1962; Gussev *et al.* 2010). The measurements of sclerotized structures examined in this study are slightly smaller than those reported by Gussev (1955, 1985), Bykhovskaya-Pavlovskaya *et al.* (1962), Anonymous (1973), Wu (1991, 2000c), and Gussev *et al.* (2010), but the ranges of the measurements overlap, and all the descriptions of the male copulatory organ are in general agreement.

3.1.3 **Discussion**

Three monogeneans, *Dactylogyrus squameus*, *Bivaginogyrus obscurus* and *Ancyrocephalus pseudorasborae*, were collected from *Pseudorasbora parva* in the native habitats of these fishes in Japan. Thus, they are considered to be native to Japan. Recently, *P. parva* is known to have invaded some of the ponds at Utabi and Yamabuse (Konishi and Takada 2013), but my samples were collected from two ponds, still inhabited only by *P. pumila* (Mayu Konishi, Shinshu University, pers. comm.). This indicates that, in these ponds at least, *B. obscurus* was not introduced, but is a native parasite of *P. pumila*. *Pseudorasbora parva* has been recorded in Hokkaidō, the Tōhoku District, and Okinawa Prefecture as a domestic alien freshwater fish (Matsuzawa and Senou 2008), and it has also been suggested that some individuals of the species were introduced from the Eurasian Continent into several rivers in Japan (Watanabe *et al*. 2000; Yoshigou 2013). Two dactylogyrids, *D. squameus* and *B. obscurus*, have spread into Europe with *P. parva* (Ondračkova *et al*. 2004; Galli *et al*. 2007; Gozlan *et al*. 2010; Anonymous 2012), and they might have become established outside of their original range on this fish in Japan as well. Many species of freshwater fish are currently known as domestic alien species in Japan (Matsuzawa and Senou 2008), but no information is available about their monogeneans. It is necessary to clarify the monogenean fauna of such domestic alien freshwater fishes.

At present, five species of *Pseudorasbora* Bleeker, 1860 are recognized as valid, and three of them, *P. parva*, *P. pumila*, and *P. pugnax* Kawase and Hosoya, 2015, are distributed in Japan (Kawase and Hosoya 2015). The latter two species are endemic to Japan and have been designated as critical endangered species by the Ministry of the Environment of Japan (Sugiyama 2015; Kawamura 2015a). To date, nothing is known about the monogenean fauna of *P. pugnax*. More study is needed on the monogeneans of these fishes because host-specific parasites of endangered hosts are sometimes threatened with co-extinction (Windsor 1990; Stork 1993; Baruš *et al.* 1997, Urabe 2010).

3.2 **Monogenean of the Kazetoge Bitterling *Rhodeus atremius atremius***

3.2.1 **Introduction**

Kazetoge bitterling, *Rhodeus atremius atremius* (Jordan and Thompson, 1914) is endemic to northern to central Kyūshū and Iki Island, western Japan, and occurs in small lowland rivers, streams, and irrigation canals (Kawamura 2015b). Recently, the species is on the verge of extinction due to artificial alteration, land consolidation, and water pollution of its habitat (Kawamura 2015b). Extinction and sudden decrease of wild hosts and alteration of local ecosystems have been suggested to cause co-extinction of their parasites (Windsor 1990; Stork 1993; Baruš *et al.* 1997, Urabe 2010), and host-specific parasites of *R. a. atremius* are likely placed in such a situation. However, the parasite fauna of this fish is currently understudied. Only seven species of trematode metacercariae have been recorded from the fish, including *Asymphylodora macrostoma* Ozaki, 1925, *Centrocestus armatus* (Tanabe, 1922), *Clonorchis sinensis* (Cobbold, 1875), *Echinochasmus japonicus* Tanabe, 1926, *Echinochasmus milvi* Yamaguti, 1939, *Exorchis oviformis* Kobayashi, 1915, and *Pseudexorchis major* (Hasegawa, 1935) (Okabe 1940; Koga 1952). In this section, a host-specific monogenean, *Dactylogyrus bicorniculus* Nitta and Nagasawa, 2016 (Dactylogyridae), is described from the gills of *R. a. atremius* in Saga Prefecture, northern Kyūshū, Japan. This new species and two species of related congeners (*Dactylogyrus bicornis* Malevitskaja, 1941 and *Dactylogyrus lophogonus* Zhang and Ji, 1980) differ from other species of the genus by a large V-shaped ventral bar and well-developed second marginal hooks. To assign the new species to the genus, molecular characterization and phylogeny of *D. bicorniculus* were provided by the help of 28S rDNA sequences, which have been used as a reliable tool to identify the dactylogyrid monogeneans and their phylogenetic relationships (*e.g.* Šimková *et al.* 2006; Mendoza-Palmero *et al.* 2015).

3.2.2 **Results**

3.2.2.1 ***Dactylogyrus bicorniculus*** Nitta and Nagasawa, 2016 (Fig. 7)

Dactylogyrus bicorniculus Nitta and Nagasawa, 2016b: 484–486, fig. 2.

Material examined. Holotype (NSMT-Pl 6185) collected on 30 March 2015. Paratypes consisting of two and five specimens (NSMT-Pl 6186 and 6187) collected on 25 May 2015 and 30 March 2015, respectively.

Description. Body (Fig. 7A) elongate, including haptor length 333±46.1 (272–413, *n*=7), width at mid-body 54± 0.3 (39–67, *n*=7). Three pairs of head organs. Two pairs of eye-spots sometimes diffused. Pharynx subspherical, length 18±2.9 (12–20, *n*=7), width 19±2.3 (14–21, *n*=7); esophagus followed by bifurcate intestine with branches confluent posterior to testis. Testis pyriform, postero-dorsal to ovary. Vas deferens arising from anterior end of testis, looping dorsoventrally around left intestine to dilate, forming seminal vesicle. Two prostatic reservoirs both saccate. Copulatory organ (Fig. 7M) sclerotized, consisting of penis and accessory piece, length 15±1.1 (12–16, *n*=8). Penis slightly curved tube, length 17±1.9 (14–19, *n*=8). Accessory piece (Fig. 7M) slightly curving along penis, and its tip holding distal end of penis, length 17±1.5 (14–19, *n*=8). Ovary in mid-body. Oviduct arising from anterior margin of ovary, continuing to oötype surrounded by Mehlis' gland. Vagina unsclerotized, opening on right lateral side, mid-length of body, leading to seminal receptacle ducting base of oötype. Vitellaria approximately co-extensive with intestine.

Haptor length 60±6.0 (50–68, *n*=7), width 100±17.3 (72–122, *n*=7). Cement gland situated base of haptor. Dorsal anchor (Fig. 7B) total length 20±2.0 (18–24, *n*=8), length to notch 13±0.6 (12–14, *n*=8), outer root length 6±0.7 (6–8, *n*=8), inner root length 11±0.9 (9–12, *n*=8), point length 4±0.5 (3–5, *n*=8). Dorsal bar (Fig. 7C) rod shape, total length 16±1.2 (14–18, *n*=8), total width 4±0.5 (3–4, *n*=8), median width 8±1.2 (6–9, *n*=8). Ventral bar (Fig. 7D) V-shaped, "bicornis" type in Gussev (1985), total length 20±1.7 (16–21, *n*=8), total width 4±0.5 (3–5, *n*=8), median width 8±1.2 (6–9, *n*=8). Hooks in 7 pairs; hook length: pair I (Fig. 7E) 15±0.7 (14–16, *n*=8); pair II (Fig. 7F) well developed, 23±1.4 (20–24, *n*=8); pair III (Fig. 7G) 20±1.4 (18–22, *n*=8); pair IV (Fig. 7H) 19±0.8 (17–19, *n*=8); pair V (Fig. 7I) 25±2.1 (20–27, *n*=8), pair VI (Fig. 7J) 22±1.4 (20–24, *n*=8); pair VII (Fig. 7K) 20±0.7 (19–21, *n*=8). Pair of needles (Fig. 7L), length 9±0.5 (9–10, *n*=8), located near second hooks.

Host. Kazetoge bittering *Rhodeus atremius atremius* (Jordan and Thompson, 1914) (Cypriniformes: Cyprinidae)

Locality. An irrigation canal flowing into the Ushitsu River, Taku city, Saga Prefecture, northern Kyūshū, Japan.

Site of infection. Gill filaments.

Prevalence and infection: *Dactylogyrus bicorniculus* was collected from *R. a. atremius* but not from a closely related bitterling, *R. ocellatus* subsp. (*n*=7). Eight (62%) of the 13 specimens of *R. a. atremius* (20.6–35.4 [mean: 29.0] mm standard length) examined were infected by 1–11 (mean: 5.4) individuals of the species.

Sequence data. PCR products of the 28S rDNA (868-bp) gene were sequenced and

submitted to GenBank (LC093099). The phylogenetic analysis based on 28S rDNA sequences suggests that the new species shows affinity with *Dactylogyrus* spp. (Fig. 8). The phylogenetic tree estimated (Fig. 8) is approximately compatible with the past analysis by Mendoza-Palmero *et al.* (2015)

Remarks. Both the large V-shaped ventral bar, named as "bicornis" type in Gussev (1985), and the well-developed second marginal hooks of *D. bicorniculus* resemble those of *D. bicornis* and *D. lophogonus* Zhang and Ji, 1980 (Malevitskaja 1941; Bykhovskaya-Pavlovskaya *et al.* 1962; Zhang and Ji 1980; Gussev 1985; Ma *et al*. 2000; Wu 2000a; Gussev *et al*. 2010). However, the penis length measured along its curved line of *D. bicorniculus* (14–19 μm) is shorter than those of *D. bicornis* (87–110 μm [Bykhovskaya-Pavlovskaya *et al.* 1962; Gussev 1985; Ma *et al*. 2000; Gussev *et al*. 2010]) and *D. lophogonus* (86–118 μm [Bykhovskaya-Pavlovskaya *et al.* 1962; Wu 2000a], 70–80 μm [Gussev 1985; Gussev *et al*. 2010]). Furthermore, the anchor total length of *D. bicorniculus* (14–18 μm) is smaller than that of *D. bicornis* (25–26 μm [Malevitskaja 1941; Ma *et al*. 2000], 25–27 μm [Bykhovskaya-Pavlovskaya *et al.* 1962], 23–27 μm [Gussev 1985; Gussev *et al*. 2010]).

3.2.3 **Discussion**

Dactylogyrus bicorniculus, *D. bicornis*, and *D. lophogonus* infect only Acheilognathinae fishes of two genera *Rhodeus* and *Acheilognathus*. These monogenean species are characterized by the large V-shaped ventral bar and well-developed second marginal hooks, but based on phylogenetic analysis of 28S rDNA fragment (Fig. 8), *D. bicorniculus* is formed a sister group with the T-shaped ventral bar that is present in *Dactylogyrus petruschewskyi* Gussev, 1955, *D. pekinensis* Gussev, 1962, *D. hypophthalmichthys* Achmerow, 1952, and *Dactylogyrus parabramis* Achmerow, 1952. While recent molecular research indicates that plural lineages are present in *Dactylogyrus* (Šimková *et al*. 2004; Chiary *et al*. 2013), molecular data are yet scarcely available on this genus consisting of about 1000 species. Combining morphological and molecular data will provide detailed information on the phylogeny of *Dactylogyrus*.

Dactylogyrus bicorniculus may face the danger of extinction with its host (*Rhodeus a. atremius*) due to its strict host-specificity to this fish: there are no record of *Dactylogyrus* from other 11 species of bitterlings inhabiting in Japan, *R. ocellatus* subsp. is the only congener occurring with *R. a. atremius* at the present sampling site, and *D. bicornis*, was not found during our examinations of *R. ocellatus* subsp. in this study and other bitterlings [*Tanakia lanceolate* (Temminck and Schlegel, 1846); *Tanakia limbata* (Temminck and Schlegel, 1846); *Pseudorhodeus tanago* (Tanaka, 1909); *Acheilognathus rhombeus* (Temminck and Schlegel, 1846); *Acheilognathus cyanostigma* Jordan and Fowler, 1903; *Acheilognathus macropterus* (Bleeker, 1871); *Acheilognathus melanogaster* Bleeker, 1860] from other localities in Japan (Nitta and Nagasawa, unpublished). A total of 167 species of freshwater fishes, including *R. a. atremius*, is listed in the Red Data Book of Japan (Hosoya 2015a). However, the parasite fauna of these fishes is poorly understood (Urabe 2010), and only 10 species of monogeneans have been reported from six species of those endangered fishes: *Gyrodactylus egusai* Ogawa and Hioki, 1986, *Gyrodactylus joi* Ogawa and Hioki, 1986, *Gyrodactylus nipponensis* Ogawa and Egusa, 1978, *Pseudodactylogyrus anguillae* (Yin and Sproston, 1948), *Pseudodactylogyrus bini* (Kikuchi, 1929), and *Pseudodactylogyrus kamegaii* Iwashita, Hirata and Ogawa 2002 from *Anguilla japonica* (Temminck and Schlegel, 1847) (Kikuchi 1929; Ogawa and Egusa 1978c; Ogawa *et al*. 1985; Ogawa and Hioki 1986; Iwashita *et al*. 2002); *Eudiplozoon nipponicum* (Goto, 1891) from *Carassius auratus grandoculis* (Temminck and Schlegel, 1846) (Kamegai, Sa. 1975b); *Discocotyle* sp. from *Hucho perryi* (Brevoort, 1856) (Ogawa 1994b); *Gyrodactylus* sp. from *Oryzias latipes* (Temminck and Schlegel, 1846) (Nagasawa *et al*. 2012); *Bivaginogyrus obscurus* (Gussev, 1955) from *Pseudorasbora pumila* Miyadi, 1930 (Nitta and Nagasawa 2014b); and *D. bicorniculus* from *R. a. atremius*. It is highly desirable to clarify the parasite fauna of the freshwater fishes on the verge of co-extinction in Japan.

Chapter 4. Alien Monogeneans from Invasive Alien Fishes in Japan

4.1 Alien Monogenean of the Channel Catfish *Ictalurus punctatus*

4.1.1 Introduction

Since 1971, the channel catfish *Ictalurus punctatus* (Rafinesque, 1818) (Siluriformes: Ictaluridae) has been transplanted to Japan from the U.S.A. multiple times for aquaculture (Maruyama *et al.* 1987). In 1982, some of the channel cat fish escaped from typhoon-damaged culture cages set in the Edo River of the Tone River system, central Honshū, and have since become established in this river system and its connecting lake, Lake Kasumigaura (Ashihara 1984; Hirata and Nagano 2000; Hanzawa 2004). Recently, the channel cat fish population has increased dramatically in this lake (Hanzawa 2004; Matsuzaki *et al.* 2011; Arayama and Iwasaki 2012). This species also has been introduced from North America to many other countries and regions of Europe and Asia for aquaculture and recreational fishing (Welcomme 1981, 1988). This section describes on the dactylogyrid monogenean *Ligictaluridus pricei* (Mueller, 1936) from the gills of *I. punctatus* in Lake Kasumigaura, Japan.

4.1.2 Results

4.1.2.1 ***Ligictaluridus pricei*** (Mueller, 1936)
(Fig. 9)

Cleidodiscus pricei Mueller, 1936: 459, 461, 464, figs 11–15; Mueller 1937: 214; Seamster 1938a: 14; Seamster 1938b: 605, 608, 610–611, figs 1–7; Summers and Bennett 1938: 248; Mizelle and Cronin 1943: 206–207, 219, 221, pl. 1: figs 65–74; Mizelle and Donahue 1944: 608–609; Mizelle and Regensberger 1945: 680–681, 697, pl. 1: figs 51–55; Sproston 1946: 233; Seamster 1948: 168; Hargis 1952: 112; Hargis 1953: 95; Mizelle and Klucka 1953: 722–723; Mizelle and Webb 1953: 208; Krueger 1954: 278; Mizelle *et al.* 1961: 634; Allison 1963: 347; Yamaguti 1963: 63, fig. 771; Žitňan 1965: 38–39, fig. 4; Hoffman 1967: 89; Lawrence and Murphy 1967: 168; Nowlin et al. 1967: 110; Molnár 1968: 301; Allison and Rogers 1970: 22, 23; Clayton and Schlueter 1970: 161; Torres and Price 1971: 132; Dechtiar 1972b: 278; Hanek and Fernando 1972a: 1307; Hanek and Fernando 1972b: 1316; Meade and Bedinger 1972: 283, 286, fig. 15; Miller *et al.* 1973: 200, 204; Prost 1973: 317–318, fig. 2; Cloutman 1974: 226, 227; Molnar *et al.* 1974: 721; Rawson and Fox 1974: 620;

Hensley and Nahhas 1975: 204; Baker and Crites 1976: 38; Bauer and Hoffman 1976: 165; Musselius *et al.* 1976: 17; Kiškaroly 1977: 202–203, fig. 7; Lambert 1977: 186, 206, 212, fig. 37; Cloutman 1978: 171–172; Riley 1978: 210; Lubinsky and Loch 1979: 2, 22; Sutherland and Holloway 1979: 130; Cone 1980: 179; Duobinis-Gray and Corkum 1985: 134; Gussev 1985: 198, 204–205, fig. 309; Hoffman 1985: 36–38, fig. 27; Musselius 1988: 147; Mirzoyeva 1988: 160–161; Bunkley-Williams and Williams 1994: 33–34, 130, fig. *Cleidodiscus pricei*; Plaisance *et al.* 2004: 427; Šimková *et al.* 2003: 5, 7, 8; Šimková *et al.* 2004: 1007; Pouyand *et al.* 2006: 245; Zhang 2012: 47, 106.

Ancyrocephalus pricei: Roman-Chiriac 1960: 88–89, fig. 59; Adamczyk 1973: 359–361, fig. 12.

Ligictaluridus pricei: Beverley-Burton 1984: 38, 40, fig. 10.2; Klassen and Beverley-Burton 1985a: 717–720, figs 2–13, table 1; Klassen and Beverley-Burton 1987: 86, fig 2; Klassen and Beverley-Burton 1988: 49; Nepszy 1988: 5, 11, 24, 37, 54, 58, 70, 80, 81; Hoffman 1999: 109, 116, fig. 170; Rosas-Valdez and Pérez-Ponce de León 2005: 222, 224; Castro 2010: 15; Pérez-Ponce de León *et al.* 2010: 30; Muzzall and Whelan 2011: 83, 117, 184, 249, 250, 289, 331, 406, 407, 460, 505; Truong 2011: 38, 64–73, 126, 153, 158, 159, 163, pls 9–11; Zhang 2012: 106; Salgado-Maldonado and Quiroz-Martínez 2013: 5, 10, 12, 16; Wang *et al.* 2013: 87–89, fig. 1.

Material examined. In total, 28 specimens (NSMT-Pl 6166) were used for the description. Soft anatomy was observed in seven specimens stained in Heidenhain's iron hematoxylin, and sclerotized structures were measured in 21 specimens fixed in ammonium picrate glycerin.

Description. Body (Fig. 9A) elongate, length 695±91.9 (554–833; *n*=13) including haptor, width at mid-body 127±13.5 (105–155; *n*=13). Cephalic glands opening on anterolateral sides of head. Two pairs of eyes. Pharynx round, diameter 34±4.9 (26–45; n=13); esophagus present; part of intestinal caeca extending to end of body and rejoining there to form elongate loop. Testis pyriform, posterodorsal to ovary. Vas deferens arising from anterior margin of testis, looping dorsoventrally around left intestinal cecum. Seminal vesicle located posterior to two saccate prostatic reservoirs. Penis (Fig. 9M, N) a slender, curved tube, length 35±2.9 (29–41; *n*=21), diameter 2±0.3 (2–3; *n*=21), diameter to length ratio 1 : 13–19. Accessory piece (Fig. 9M, N) 33±2.3 (29–38; *n*=21) in length, touching base of penis (i.e., concave portion near base of accessory piece fitting base of penis) and extending to tip of penis, twisted one time near tip and also at mid-length, usually straight in overall shape (Fig. 9M), but in a few specimens bent in middle

(Fig. 9N). Ovary in mid-body, ovoid. Oviduct arising from anterior side of ovary, continuing as oötype and uterus. Mehlis' gland connecting lowest part of oötype. Vagina exiting from left side of oviduct, running between vas deferens and left intestinal caecum to vaginal opening on left side of ventral body surface. Vitellaria approximately co-extensive with intestinal caeca.

Haptor length 79±13.0 (60–100; *n*=13), width 107±12.7 (89–129; *n*=13). Each hamulus lacking deep root. Dorsal hamuli (Fig. 9B) smaller than ventral hamuli, total length 45±3.0 (40–49; *n*=21), length to notch 43±2.2 (39–48 *n*=21), superficial root length 13±1.5 (10–16; *n*=21), blade length 18±1.1 (15–20; *n*=21). Ventral hamuli (Fig. 9C) with total length 51±2.4 (46–55; *n*=21), length to notch 47±1.9 (44–50; *n*=21), superficial root length 15±1.6 (12–18; *n*=21), blade length 18±1.6 (15–21; *n*=21). Dorsal bar (Fig. 9D) with lamella-like flange at midsection, length 49±3.0 (42–54; *n*=21), median width 10±1.7 (7–13; *n*=21). Ventral bar (Fig. 9E) V-shaped, length 45±2.4 (41–50; *n*=21), median width 7±1.2 (6–11; *n*=21). Marginal hooks of larval type, 7 pairs; hook pair I, hook pair II, and hook pairs III–VII located at center, tip, and each side of haptor, respectively (Fig. 9A); in length, pair I (Fig. 9E) 14±0.8 (13–16; *n*=16); pair II (Fig. 9F) 12±0.8 (11–13; *n*=16), smallest; pair III (Fig. 9G) 15±0.8 (14–17; *n*=16); pair IV (Fig. 9H) 15±0.7 (14–16; *n*=16); pair V (Fig. 9I) 15±0.6 (14–16; *n*=16), pair VI (Fig. 9J) 15±0.4 (14–16; *n*=16); pair VII (Fig. 9K) 15±0.4 (15–16; *n*=16).

Host. Channel catfish *Ictalurus punctatus* (Siluriformes: Ictaluridae).

Locality. Lake Kasumigaura, Okijuku-machi, Tsuchiura city, Ibaraki Prefecture, Japan.

Site of infection. Gill filaments.

Remarks. This monogenean was originally described by Mueller (1936) as *Cleidodiscus pricei* from *Ictalurus punctatus*, *Ameiurus nebulosus* (Lesueur, 1819) (as *I. meiurus nebulosus*), and *A. natalis* (Lesueur, 1819) (as *I. natalis*) (Siluriformes: Ictaluridae) in Florida, U.S.A. It was transferred to the genus *Ligictaluridus* by Beverley-Burton (1984). The specimens examined in this study approximately conform to the descriptions of *L. pricei* by Mueller (1936), Mizelle and Cronin (1943), Mizelle and Regensberger (1945), Prost (1973), Kiškaroly (1977), Žitňan (1965), Gussev (1985), Klassen and Beverley-Burton (1985a, b), Truong (2011), and Wang *et al*. (2013). The sclerotized structures of *L. pricei* are known to show marked variation in morphology and measurements (Seamster 1938b, Mizelle and Cronin 1943, Mizelle and Donahue 1944, Mizelle and Regensberger 1945), but Mizelle and Donahue (1944) suggested that such variation is caused by differences in fixation method. On the other hand, the length of the accessory piece reported by Hargis (1953) is quite short: 10–18 µm. He presented no drawings of the accessory piece, but since it is sometimes bent (cf. Prost 1973: fig. 2f, this study: fig. 2N), Hargis (1953) probably measured a bent one. Until now, the vagina has not been described clearly, because it is obscured by well-developed vitellaria (Klassen and Beverley-Burton 1985a). Based on the specimens stained in Heidenhain's iron hematoxylin, the present study has revealed that it runs between the vas deferens and the left intestinal caecum (Fig. 9A).

At present, the genus *Ligictaluridus* consists of six valid species (Klassen and Beverley-Burton 1985a, b): *L. bychowskyi* (Price and Mura, 1969), *L. floridanus* (Mueller, 1936), *L. mirabilis* (Mueller, 1937), *L. monticellii* (Cognetti de Martiis, 1924), *L. posthon* Klassen, Beverley-Burton and Dechtiar, 1985, and *L. pricei*. *Ligictaluridus pricei* is readily separated from *L. monticellii* by the presence of a deep root (Klassen and Beverley-Burton 1985a) on each hamulus. The distal limb of the accessory piece has a single terminal projection in *L. pricei*, while those of *L. floridanus* and *L. mirabilis* have two and four terminal projections, respectively (Mueller 1936, 1937; Klassen and Beverley-Burton 1985a). Unlike *L. pricei*, *L. bychowskyi* has a tapered penis (Price and Mura 1969; Klassen and Beverley-Burton 1985a). *Ligictaluridus pricei* and *L. posthon* are separated from each other by the diameter to length ratio of the penis: 1 : 18 (Klassen and Beverley-Burton 1985b) or 1 : 13–19 (this study) for *L. pricei* versus 1 : 6 (Klassen and Beverley-Burton 1985b) for *L. posthon*.

Roman-Chiriac (1960) reported a monogenean as *Ancyrocephalus pricei* (Mueller, 1934) Mizelle and Cronin, 1943, an attribution later repeated by Adamczyk (1973). However, Mueller (1934a, b) did not describe the species, nor did Mizelle and Cronin (1943) transfer it to *Ancyrocephalus*. Rather, Mueller (1936) described it, and it has recently been placed in *Ligictaluridus* (Beverley-Burton 1984). Specimens reported by Dechtiar (1972a) as *Cleidodiscus pricei* from the stonecat *Noturus flavus* Rafinesque, 1818 (Siluriformes: Ictaluridae) were regarded as *Ligictaluridus posthon* by Klassen and Beverley-Burton (1985b).

4.1.3 **Discussion**

While *L. pricei* is native to North America, it has been co-introduced with fishes of the family Ictaluridae into the Eurasian continent and the West Indies (Table 4). Similarly in Lake Kasumigaura, this monogenean has most likely become established along with channel catfish from the U.S.A. Recently, the fish has spread to and become established in other waters of Japan (Katano *et al*. 2010), and the monogenean has likely accompanied it. Originally, *L. pricei* was widely and continuously distributed in temperate and subarctic areas of North America (Table 5), ranging from 25°14′N (Nazas River, Mexico: Pérez-

Ponce de León *et al*. 2010) to 49°07′N (Lake of the Woods, Canada: Dechtiar 1972b). These climates and latitudes overlap with those of the Japanese Archipelago, which implies that *L. pricei* has the capacity to become established throughout Japan. More study is necessary in order to determine the geographical distribution of this monogenean in Japan.

To date, *L. pricei* has been recorded from 11 species and four genera of ictalurids (Tables 4, 5) and is known to cause disease in cultured catfish (Hoffman 1985). It has also been reported from three species in two families of Perciformes: the green sunfish *Lepomis cyanellus* Rafinesque, 1819; the warmouth *L. gulosus* (Cuvier, 1829) (Centrarchidae); and the striped bass *Morone saxatilis* (Walbaum, 1792) (Moronidae) (Allison and Rogers 1970; Hensley and Nahhas 1975). According to Allison and Rogers (1970), the green sunfish collected in a pond in which cultured channel catfish were densely stocked and became heavily infected by *L. pricei*. These authors regarded this infection as “undoubtedly a case of accidental parasitism”, because the monogenean disappeared from the green sunfish after the catfish were killed. In light of this observation, it is possible that *L. pricei* also infects native fishes in Lake Kasumigaura, where the catfish is very abundant (Arayama and Iwasaki 2012). The monogenean fauna of Lake Kasumigaura is almost completely unknown, with only four species previously recorded: *Eudiplozoon nipponicum* (Goto, 1891) (as *Diplozoon nipponicum*) (Diplozoidae) has been reported from *Cyprinus carpio* Linnaeus, 1758 (Cypriniformes: Cyprinidae) (Kamegai 1968), and *Bivaginogyrus obscurus*, *Dactylogyrus squamous* Gussev, 1955, and *Ancyrocephalus pseudorasborae* Achmerow, 1952 (Gussev, 1955) (Dactylogyridae) from *Pseudorasbora parva* (Temminck and Schlegel, 1846) (Cypriniformes: Cyprinidae) (Nitta and Nagasawa 2014b, 2016a). Infection by alien monogeneans sometimes poses a high risk for native fish resources (Petrushevski and Shulman 1970; Johnsen and Jensen 1986; Ogawa 2005, 2010; Taraschewski 2006; Yoshinaga *et al*. 2009), so it is necessary to clarify and monitor the monogenean fauna of this lake.

4.2 **Alien Monogeneans of the Vermiculated Sailfin Catfish *Pterygoplichthys disjunctivus***

4.2.1 **Introduction**

Armored catfishes of the family Loricariidae (Actinopterygii: Siluriformes) are popular in Japan as ornamental aquarium fish and are imported into this country through the tropical fish trade (Matsuzawa and Senou 2008). The vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Weber, 1991), of South American origin, is one of such armored catfish and, since the 1980s, it has become established in rivers on Okinawa Island, southern Japan (Takeshima and Yoshino 1996; Tachihara *et al*. 2002). It has also become established in several states of the U.S.A. (Texas, Florida, and Nevada), Taiwan, the Philippines, Indonesia, Singapore, and Turkey (Hoover *et al*. 2004; Chavez *et al*. 2006; Page and Robins 2006; Özdilek 2007; Gibbs *et al*. 2008).

Four species of monogeneans are known to have been introduced with armored catfishes into India and China (Jogunoori *et al.* 2004; Li *et al.* 2009; Li and Huang 2012). This section describes on the dactylogyrid monogeneans *Unilatus unilatus* Mizelle and Kritsky, 1967, *U. brittani* Mizelle, Kritsky, and Crane, 1968, *Trinigyrus peregrinus* Nitta and Nagasawa, 2016, and *Heteropriapulus heterotylus* (Jogunoori, Kritsky, and Venkatanarasaiah, 2004), parasitic on the gills of *P. disjunctivus* from Okinawa island, southern Japan.

4.2.2 **Results**

4.2.2.1 ***Unilatus unilatus*** Mizelle and Kritsky, 1967

(Fig. 10)

Unilatus unilatus Mizelle and Kritsky, 1967: 1113–1114, figs 1–8; Mizelle *et al*. 1968: 191, figs 1–9; Kohn and Cohen 1998: 1533; Kohn and Pinto Paiva 2000: 38; Thatcher 2006: 89, fig. 3-58; Li *et al.* 2009: 599, figs 1-4, 2-1–5; Mendoza-Palmero *et al.* 2012: 493–495, figs 48–54; Zica *et al*. 2012: 88–90, figs 1–2; Branches and Domingues 2014: 92.

Unilatus brevispinus Suriano, 1985: 170–172, figs 9–15; Kohn and Cohen 1998: 1533; Kohn and Pinto Paiva 2000: 38; Thatcher 2006: 89.

Material examined. Eleven specimens were used for the description: two specimens stained in Heidenhain's iron hematoxylin (NSMT-Pl 6188) from the Sembaru Reservoir, and five and four specimens fixed in APG (NSMT-Pl 6189 and 6190–6191) from the Hija River and the Sembaru Reservoir, respectively.

Additional specimens. Eleven specimens from the Sembaru Reservoir (RUMF-ZF-00009–00010a).

Description. Body (Fig. 10A) elongate, length 1263±312.3 (768–1832, *n*=8) including haptor, width at mid-body 164±31.3 (123–221, *n*=8). Cephalic glands opening on anterolateral sides of head. Eyes dispersed. Alimentary system consisting of spherical pharynx (length 54±9.9 [38–68, *n*=8], width 48±8.7 [36–64, *n*=8]), esophagus, and bifurcate intestinal caeca united posterior to ovary. Testis elongate, in mid-body, intercaecal, posterior to ovary, length 131±31.1 (109–153, *n*=2), width 38±11.3 (30–46, *n*=2). Vas deferens arising from anterior margin of testis, looping dorsoventrally around left intestinal caecum. Seminal vesicle a simple dilation of vas deferens, lying along ventral body midline. Two prostatic reservoirs immediately anterior to seminal vesicle, saccate: dorsal prostatic reservoir length 40±6.4 (35–44, *n*=2), width 17±6.4 (12–21, *n*=2); ventral prostatic reservoir length 54±4.2 (51–57, *n*=2), width 23±4.2 (51–57, *n*=2). Male copulatory organ (Fig. 10M) consisting of penis and accessory piece. Penis (Fig. 10M) sclerotized, length 89±3.9 (82–96, *n*=10), spiral counterclockwise; distal medial portion with small bulb; distal portion thin and spiral. Accessory piece (Fig. 10M) length 64±3.5 (58–68, *n*=10), rod-shaped, distal end bent and serving as guide for male copulatory organ. Ovary elongate, in mid-body, intercaecal, length 218±53.0 (180–255, *n*=2), width 59±14.1 (49–69, *n*=2). Oviduct arising from anterior side of ovary, continuing as oötype surrounded by thick glandular wall. Mehlis' gland not observed. Vagina (Fig. 10N) well sclerotized, funnel-shaped, length 24±1.4 (22–26, *n*=9), exiting from ventral side of seminal reservoir to opening on ventral body surface. Seminal reservoir located left of oviduct, with its duct leading into left side of oviduct. Vitellaria approximately co-extensive with intestinal caeca.

Haptor length 104±22.3 (72–133, *n*=8), width 131±26.2 (94–175, *n*=8). Anterior anchor (Fig. 10B) larger than posterior anchor, total length 47±3.6 (42–51, *n*=10), outer length 36±2.6 (33–41, *n*=10), base width 16±1.2 (14–18; *n*=10), point length 21±1.1 (19–23, *n*=10); accessory structure (length 12±1.2 [10–14, *n*=8], width 2±0.5 [2–3, *n*=8]) connected to inner root by thin fiber. Posterior anchor (Fig. 10C) with sclerotized cap (length 17±1.1 [16–19, *n*=10]) of outer base, total length 24±2.5 (21–28, *n*=10), outer length 23±1.9 (21–26, *n*=10), base width 16±1.5 (14–19, *n*=10), point length 21±1.1 (8–9, *n*=10). Anterior bar (Fig. 10D) broadly V-shaped, length 42±4.0 (39–49, *n*=10), total width 15±1.1 (13–17, *n*=10), median width 9±2.8 (5–13, *n*=10). Posterior bar (Fig. 10E) broadly V-shaped with bulge at midsection, length 49±4.9 (42–57, *n*=10), total width 17±3.0 (12–21, *n*=10), median width 9±1.9 (6–11, *n*=10). Marginal hooks of larval type, 7 pairs; in length, pair I (Fig. 10F) 11±0.6 (10–12, *n*=9), smallest; pair II (Fig. 10G) 16±1.2 (15–19, *n*=9); pair III (Fig. 10H) 16±0.8 (15–17, *n*=9); pair IV (Fig. 10I) 16±0.9 (15–18, *n*=9); pair V (Fig. 10J) 16±0.7 (15–17, *n*=9); pair VI (Fig. 10K); 14±0.7 (12–14, *n*=9) 16±0.7 (15–17, *n*=9); pair VII (Fig. 2L) 19±0.7 (17–19, *n*=9).

Host. Vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Siluriformes: Loricariidae).

Localities. The Hija River, Misato, Okinawa city; Sembaru Reservoir, Sembaru, Nishihara town, Okinawa-jima island, Okinawa Prefecture.

Site of infection. Gill filaments.

Prevalence and intensity range (mean). 50% (5/10) and 1–8 (3.0) in the Hija River; 80% (4/5) and 5–45 (26.3) in the Sembaru Reservoir.

Sequence data. A BLAST search of a 928-bp sequence that spanned the partial 28S rDNA region (accession no. LC104307) did not have any identical hits. The closest hits showed 90–91% similarity with the following species: *Demidospermus mortenthaleri* Mendoza-Palmero, Scholz, Mendoza-Franco, and Kuchta, 2012 (KP056245, KP056246), *Ameloblastella chavarriai* (Price, 1938) (KP056251), *Thaparocleidus vistulensis* (Siwak, 1932) (AJ969941), *T. infundibulovagina* (Yamaguti, 1942) (EF100548), and *T. varicus* (Achmerow, 1952) (DQ157668).

Remarks. Mizelle and Kritsky (1967) originally described *Unilatus unilatus* from *Hypostomus* sp. (as *Plecostomus* sp.) (Siluriformes: Loricariidae) imported to the Steinhart Aquarium in San Francisco from the Amazon River Basin (no information on the country). Subsequently, this species has been reported from the following five species of loricariid: *Hypostomus* sp. from the Amazon River Basin, Brazil (Mizelle *et al*. 1968); *Pterygoplichthys anisitsi* Eigenmann and Kennedy, 1903 from Iquitos-Belén, Peru (Mendoza-Palmero *et al*. 2012); *Hypostomus iheringii* (Regan, 1908), *H. regani* (Ihering, 1905), and *H. strigaticeps* (Regan, 1907) from São Paulo, Brazil (Zica *et al*. 2012). *Unilatus brevispinus* described by Suriano (1985) from *Pterygoplichthys multiradiatus* (Hancock, 1828) in the Rio Negro, Brazil, was synonymized with *U. unilatus* by Mendoza-Palmero *et al*. (2012). In addition, *U. unilatus* is known as an alien parasite co-introduced with *Hypostomus plecostomus* (Linnaeus, 1758) into Guangdong, China (Li *et al*. 2009). The present collection in Japan represents a new country record for *U. unilatus*, and *P. disjunctivus* is a new host record for this monogenean.

The measurements and morphology of sclerotized parts of the specimens collected in the present study are almost identical to the descriptions of *U. unilatus* by Mizelle and Kritsky (1967), Mendoza-Palmero *et al*. (2012), and Zica *et al*. (2012). At present, *Unilatus* consists of six valid species: *U. unilatus*; *U. anoculus* (Price, 1968); *U. brittani* Mizelle, Kritsky, and Crane, 1968; *U. dissimilis* Suriano, 1985; *U. irae* Branches and Domingues, 2014; and *U. scaphirhynchae* Suriano, 1985. *Unilatus unilatus* is distinguished from *U. brittani* by the posterior anchor having a sclerotized cup and a shorter blade than its base (Fig. 10C); the length of the vagina, 22–26 μm (this study) for *U. unilatus* versus 7–8 μm (this study) for *U. brittani*; and the posterior bar, which in *U. brittani* is more than twice as long as the anterior bar. The posterior anchor's total length in *U. unilatus* (19–22 µm: Mizelle and Kritsky 1967; 21–23 µm: Suriano 1985; 24–25 µm: Mendoza-Palmero *et al*. 2012; 23–25 µm: Zica *et al*. 2012; 21–28 µm: this study) is less than those of *U. anoculus* (35–39 µm: Price 1968a) and *U. irae* (41–47 µm: Branches and Domingues 2014). By the total length of the posterior bar, *U. unilatus* (38–44 µm: Mizelle and Kritsky 1967; 31–35 µm: Suriano 1985; 52–58 µm: Mendoza-Palmero *et al*. 2012; 49–59 µm: Zica *et al*. 2012; 42–57 µm: this study) is separable from *U. anoculus* (63–69 µm: Price 1968a), *U. dissimilis* (21–23: in Suriano 1985), and *U. scaphirhynchae* (14–17 µm: Suriano 1985).

4.2.2.2 ***Unilatus brittani*** Mizelle, Kritsky, and Crane, 1968
(Fig. 11)

Unilatus brittani Mizelle, Kritsky, and Crane, 1968: 192, figs 10–18; Suriano 1985: 165–168, figs 1–8; Kohn and Cohen 1998: 1532; Thatcher 2006: 89; Mendoza-Palmero *et al*. 2012: 493, figs 44–47; Branches and Domingues 2014: 92.

Unilatus longispinus Suriano, 1985: 172, figs 16–21; Kohn and Cohen 1998: 1533; Thatcher 2006: 89.

Material examined. Only sclerotized structures were observed in two specimens (NSMT-Pl 6193a and 6194a together with five specimens of *H. heterotylus*) fixed in APG.

Description. Body elongate, length 367±21.2 (352–382, *n*=2) including haptor, width at mid-body 108±7.8 (102–113, *n*=2). Male copulatory organ (Fig. 11L) consisting of penis and accessory piece. Penis (Fig. 11L) sclerotized, length 38±1.4 (37–39, *n*=2), spiral counterclockwise; distal medial portion with small bulb; distal portion thin; basal portion curved. Accessory piece (Fig. 11L) 29±2.1 (27–30, *n*=2) in length, rod-shaped, distal end bifid and holding tip of male copulatory organ. Vagina (Fig. 11M) sclerotized, funnel-shaped, length 8±0.7 (7–8, *n*=2).

Haptor length 68±8.5 (62–74, *n*=2), width 118±0.7 (117–118, *n*=2). Anterior anchor (Fig. 11A) smaller than posterior anchor, total length 26±0.7 (25–26, *n*=2), outer length 20±0.7 (19–20, *n*=2), base width 7±0.7 (6–7, *n*=2), point length 13±1.4 (12–14, *n*=2), lacking accessory structure. Posterior anchor (Fig. 11B) lacking sclerotized cap and root, total length 34±0.7 (33–34, *n*=2), base width 9±0.7 (8–9, *n*=2), point length 13±1.4 (12–14, *n*=2). Anterior bar (Fig. 11C) broadly V-shaped, with expanded midsection, length 17±1.4 (16–18, *n*=2), total width 9±0.7 (8–9, *n*=2), median width 6±0.7 (5–6, *n*=2). Posterior bar (Fig. 11D) with curved ends, length 59±0.0 (59, *n*=2), total width 8±0.7 (7–8, *n*=2), median width 6±0.7 (5–6, *n*=2). Marginal hooks of larval type, 7 pairs; in length, pair I (Fig. 11E) 13±0.7 (12–13, *n*=2); pair II (Fig. 11F) 14±0.7 (13–14, *n*=2); pair III (Fig. 11G) 13±0.0 (13, *n*=2); pair IV (Fig. 11H) 13±1.4 (12–14, *n*=2); pair V (Fig. 11I) 12±0.7 (11–12, *n*=2); pair VI (Fig. 11J) 14±0.7 (13–14, *n*=2); pair VII (Fig. 11K) 13±0.0 (13, *n*=2).

Host. Vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Siluriformes: Loricariidae).

Locality. The Hija River, Misato, Okinawa city, Okinawa-jima island, Okinawa Prefecture.

Site of infection. Gill filaments.

Prevalence and intensity range (mean). 20% (2/10) and 1 (1.0).

Remarks. This monogenean was originally described by Mizelle *et al.* (1968) from *Hypostomus* sp. (as *Plecostomus* sp.) in the Amazon River Basin, Brazil. Later, this species was reported from *Hypostomus* sp. in São Paulo, Brazil (Suriano 1985) and from *Pterygoplichthys anisitsi* in Iquitos-Belén, Peru (Mendoza-Palmero *et al*. 2012). *Unilatus longispinus* described by Suriano (1985) from *P. multiradiatus* was regarded as a junior synonym of *U. brittani* by Mendoza-Palmero *et al*. (2012). The morphology and measurements of the male copulatory organ and haptoral structures of the specimens examined in this study conform to the descriptions of *U. brittani* by Mizelle *et al*. (1968), Suriano (1985), and Mendoza-Palmero *et al*. (2012). This is the first record of *U. brittani* in Japan and *P. disjunctivus* represents a new host record for this monogenean.

Unilatus brittani is separated from *U. unilatus* by the posterior anchor's lack of a sclerotized cup and its having a longer blade than its base (Fig. 11B), the length of the vagina, and the anterior bar being more than twice as long as the posterior bar (see Remarks for *U. unilatus*). The length of the posterior bar in *U. brittani* (59–64 μm: Mizelle *et al*. 1968; 60–66 μm: Suriano 1985; 57–72 μm: Mendoza-Palmero *et al*. 2012; 59 μm: this study) is greater than that of *U. dissimilis* (21–23 μm: Suriano 1985) and *U. scaphirhynchae* (14–17 μm: Suriano 1985) but shorter than that of *U. irae* (82–95 μm: Branches and Domingues 2014). By the length of the penis, *U. brittani* (52–55 μm: Mizelle *et al*. 1968; 17–35 μm: Suriano 1985; 33–37 μm: Mendoza-Palmero *et al*. 2012; 37–39 μm: this study) differs from *U. anoculus* (61–66 μm: Price 1968a) and *U. irae* (65–67 μm: Branches and Domingues 2014).

4.2.2.3 ***Trinigyrus peregrinus*** Nitta and Nagasawa, 2016

(Fig. 12)

Trinigyrus peregrinus Nitta and Nagasawa, 2016c: 100–102, fig. 4.

Material examined. Holotype: NSMT-Pl 6195 fixed in APG from the Hija River on 25 June 2015. Paratypes: Twenty-two specimens: four and two specimens stained in Heidenhain's iron hematoxylin from the Hija River (NSMT-Pl 6196–6197) and the Sembaru Reservoir (NSMT-Pl 6203), respectively; and nine and seven specimens fixed in APG from the Hija River (NSMT-Pl 6198–6200) and the Sembaru Reservoir (NSMT-Pl 6201–6202), respectively.

Additional specimens. Two and four specimens from the Hija River (RUMF-ZF-00010b–00011) and the Sembaru Reservoir (RUMF-ZF-00012), respectively.

Description. Body (Fig. 12A) subconical, length 647±119.8 (460–819, *n*=18) including haptor, width at mid-body 217±46.9 (148–321, *n*=18). Alimentary system consisting of ovate pharynx (length 39±6.6 [25–52, *n*=21], width 40±9.3 [25–55, *n*=21]), short esophagus, and bifurcate intestinal ceca united posterior to testis. Testis pyriform, in mid-body, intercaecal, posterior to ovary, length 75±15.6 (62–102, *n*=5), width 89±4.8 (84–94, *n*=8). Vas deferens arising from anterior margin of testis, looping dorsoventrally around left branch of intestinal cecum, distending to form seminal vesicle, and entering base of male copulatory organ. Two prostatic reservoirs saccate, located to right of oötype. Male copulatory organ (Fig. 12E) consisting of penis and accessory piece. Penis (Fig. 12E) a coiled tube, forming circle of diameter 25±3.8 (21–36, *n*=19), curve length 60±2.5 (55–64, *n*=19). Accessory piece (Fig. 12E) c-shaped, length 31±3.2 (25–38, *n*=20), not articulating with male copulatory organ. Ovary in mid-body. Oviduct arising from anterior side of ovary, continuing as oötype surrounded by thick wall and located left of prostatic reservoirs. Mehlis' gland not observed. Seminal reservoir located left of oviduct, opening to left side of oviduct. Vagina unsclerotized, exiting from anterior side of seminal reservoir, running ventrally to vaginal opening on right lateral side of body surface. Vitellaria approximately co-extensive with intestinal caeca. Egg (Fig. 12F) ovate, length 63±11.7 (50–72, *n*=3), width 32±4.0 (28–36, *n*=3), with long filament (about 4.5 mm, *n*=1) coiled in oötype.

Haptor with 5 pairs of haptoral appendages, length 158±24.2 (130–195, *n*=18), width 342±72.4 (230–435, *n*=18). Pair of anchors (Fig. 12B) with subrectangular base, total length 64±3.4 (59–71, *n*=22), base width 17±1.3 (15–20, *n*=20), point length 4±0.5 (3–5, *n*=21). Bar (Fig. 12C) broadly W-shaped, total length 154±13.7 (126–178, *n*=22), total width 38±4.5 (30–45, *n*=22), median width 4±0.7 (3–6, *n*=22). Marginal hooks (Fig. 12D) of larval type, 7 pairs, all of approximately same length, 13±0.8 (11–14, *n*=22).

Host. Vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Siluriformes: Loricariidae).

Localities. The Hija River, Misato, Okinawa city; Sembaru Reservoir, Sembaru, Nishihara town, Okinawa-jima island, Okinawa Prefecture.

Sites of infection. Gill rakers, arches, and filaments.

Prevalence and intensity range (mean). 40% (4/10) and 4–13 (8.5) in the Hija River, and 100% (5/5) and 4–9 (6.4) in the Sembaru Reservoir.

Sequence data. A BLAST search of a 954-bp sequence that spanned the partial 28S rDNA region (accession no. LC104308) did not have any identical hits. The closest hits showed an 89–90% similarity with the following species: *Ancyrocephalus percae* (Ergens 1966) (KF499080), *A. paradoxus* Creplin, 1839 (AJ969952), *Thaparocleidus siluri* (Zandt, 1924) (AJ969940), *T. vistulensis* (AJ969941), *Euryhaliotrema johni* (Tripathi, 1959) (DQ157657), *Urocleidus similis* (Mueller, 1936) (AJ969951), and *Actinocleidus recurvatus* Mizelle and Donahue, 1944 (AJ969951).

Remarks. The specimens examined in this study conform to the generic diagnosis of *Trinigyrus* as emended by Kritsky *et al.* (1986). Currently, four species are assigned to this genus: *T. acuminatus* Kritsky, Boeger, and Thatcher, 1986; *T. hypostomatis* Hanek, Molnar, and Fernando, 1974; *T. mourei* Boeger and Belmont-Jegu, 1994; and *T. tentaculoides* Kritsky, Boeger, and Thatcher, 1986. *Trinigyrus peregrinus* is readily separated from *T. acuminatus*, which has an elongate cirrus and a complex accessory piece (Kritsky *et al.* 1986). The new species with its c-shaped accessory piece is also readily distinguishable from *T. tentaculoides* and *T. mourei*, both of which have a J-shaped accessory piece (Kritsky *et al.* 1986; Boeger and Belmont-Jegu 1994). The male copulatory organ of *T. peregrinus* is coiled and forms a circle, while that of *T. hypostomatis* is J-shaped and tapers distally (Hanek *et al.* 1974). Furthermore, the accessory piece articulates with the base of the penis in *T. hypostomatis* (Hanek *et al.* 1974; Boeger and Belmont-Jegu 1994), but not (or at least not clearly) in *T. peregrinus*.

Li *et al.* (2009) showed eggs of *Trinigyrus hypostomatis* with a short filament (fig. 1-4) and *Unilatus unilatus* with a long coiled filament (fig. 2-6), but they appear to have gotten the species (or their eggs) confused, because *U. unilatus* has an egg with a short filament (Zica *et al.* 2012) whereas *T. peregrinus* has an egg with a long filament (this study).

4.2.2.4 ***Heteropriapulus heterotylus*** (Jogunoori, Kritsky, and Venkatanarasaiah, 2004) (Fig. 13)

Heterotylus heterotylus Jogunoori, Kritsky, and Venkatanarasaiah, 2004: 116–117, figs 1–7.

Heteropriapulus heterotylus: Kritsky 2007: 233; Li and Huang 2012: 117–119, fig. 2; Nitta and Nagasawa 2013: 281–283, fig. 2; Rodríguez-Santiago *et al*. 2015: 58–61.

Material examined. Six, five, and fifteen specimens collected from the Asatomata River (RUMF-ZF-00013), the Hija River (NSMT-Pl 6193b, 6194b together with two specimens of *U. brittani*), and the Sembaru Reservoir (NSMT-Pl 6030, RUMF-ZF-00014), respectively.

Description. Body (Fig. 13A) including haptor length 249±50.7 (183–353; *n*= 9), width at mid-body 92±21.1 (68–126; *n*=9). Three pairs of head organs. Eye-spots dissociated. Alimentary system consisting of subspherical pharynx (length 22±3.1 [17–25; *n*=7], width 19±3.9 [13–14, *n*=7]), esophagus, and bifurcate intestinal caeca united posterior to testis. Testis pyriform, in mid-body, intercaecal, posterior to ovary. Vas deferens arising from anterior margin of testis, looping dorsoventrally around left intestinal caecum, distending to form seminal vesicle, and entering base of male copulatory organ. Two prostatic reservoirs saccate. Male copulatory organ (Fig. 13G) consisting of penis and accessory piece. Penis (Fig. 13G) with rounded base, total length 41±3.4 (37–47; *n*=10). Sclerotized accessory piece (Fig. 13G) consisting of four subunits, length 30±2.3 (28–36; n=10). Ovary in mid-body. Oviduct arising from anterior side of ovary, continuing as oötype. Mehlis' gland not observed. Vagina (Fig. 13H) tubular, sclerotized; vaginal pore located mid-body on ventral body surface.

Haptor length 49± 10.4 (25–64; n=9), width 90±13.5 (77–120; *n*=9). Dorsal anchor (Fig. 13B), total length 20±0.6 (19–21, *n*=8), shaft length 14±0.5 (13–14; *n*=10), outer root absent, inner root length 7±0.5 (6–8; *n*=10), point length 11±0.8 (9–12; *n*=10). Ventral anchor (Fig. 13C), total length 39±0.9 (38–40; *n*=8), anchor patch length 5±1.5 (3–7; *n*=7), point length 1±0.0 (*n*=8). Anchor filaments not observed. Dorsal bar (Fig. 13D) total length 21± 1.1 (20–23; *n*=8), total width 3±0.5 (3–4; *n*=8), median width 1±0.5 (1–2; *n*=8). Ventral bar (Fig. 13E) total length 48±2.7 (44–53; *n*=8), total width 13±0.7 (12–14; *n*=8), median width 4±0.5 (4–5; *n*=8). Hooks (Fig. 13F) of larval type, 7 pairs, all of approximately same length, hook length 13± 0.7 (12–14; *n*=10).

Host. Vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (Siluriformes: Loricariidae).

Localities. The Asatomata River, Miyagusuku, Haebaru town; the Hija River, Misato, Okinawa city; Sembaru Reservoir, Sembaru, Nishihara town, Okinawa-jima island, Okinawa Prefecture.

Site of infection. Gill filaments.

Prevalence and intensity (mean). 100% (2/2) and 3–9 (6) in the Asatomata River;

90% (9/10) and 1–5 (2.6) in the Hija River; 60% (3/5) and 2–45 (16.3) in the Sembaru Reservoir.

Remarks. The present species was originally described by Jogunoori *et al*. (2004) as *Heterotylus heterotylus* from the gills of *Hypostomus* sp. (Siluriformes: Loricariidae), an armored catfish that had been introduced into India via the aquarium fish trade. *Heterotylus* Jogunoori, Kritsky, and Venkatanarasaiah, 2004, however, is a junior homonym of the weevil genus *Heterotylus* Kirsch in Reitter, 1913, and Kritsky (2007) proposed the new replacement name *Heteropriapulus* Kritsky, 2007 to accommodate this parasite. Recently, *H. heterotylus* was also reported from China with the suckermouth catfish *Hypostomus plecostomus* (Linnaeus, 1758) (Li and Huang 2012) and Mexico with *P. disjunctivus* (Rodríguez-Santiago *et al*. 2015). The morphology and measurements of the specimens collected in this study agree with those of the species reported by Jogunoori *et al*. (2004) from India and by Li and Huang (2012) from China.

4.2.3. **Discussion**

Monogeneans of the genera *Unilatus*, *Trinigyrus*, and *Heteropriapulus* have been reported only from loricariids (Mizelle and Kritsky 1967; Mizelle *et al*. 1968; Hanek *et al*. 1974; Kritsky *et al*. 1986; Suriano 1985; Boeger and Belmont-Jegu 1994; Jogunoori *et al*. 2004, Mendoza-Palmero *et al*. 2012; Li and Huang 2012, Zica *et al*. 2012, Rodríguez-Santiago *et al*. 2015), and only *Pterygoplichthys disjunctivus* is loricariid established into the Okinawa-jima island (Takeshima and Yoshino 1996; Tachihara *et al*. 2002). Thus, the four monogeneans found in this study, *U. unilatus*, *U. brittani*, *T. peregrinus*, *H. heterotylus*, are considered to have been co-introduced together with *P. disjunctivus* to Okinawa-jima island. In this study, four, three, and one species of these monogeneans were found on *P. disjunctivus* from the Hija River, Sembaru Reservoir, and Asatomata River, respectively. More examination of *P. disjunctivus* from more sites on this island may clarify the distributional range expansion of these monogeneans on the island.

Pterygoplichthys disjunctivus was reported as an alien species in Mexico, where its monogenean fauna was well studied in Campeche (Rodríguez-Santiago *et al*. 2015). Interestingly, only *H. heterotylus* was found there, but four species of monogenean including this species were found on Okinawa-jima island in the present study. This difference between two the countries in the monogenean fauna of the same host fish may possibly be due to differences in its manner of introduction to individual countries and/or in the water environment there. Since *U. unilatus*, *U. brittani*, and *H. heterotylus* have a wide host-specificity to loricariids (Mizelle and Kritsky 1967; Mizelle *et al*. 1968;

Suriano 1985; Jogunoori *et al*. 2004; Li *et al*. 2009; Mendoza-Palmero *et al*. 2012; Li and Huang 2012; Zica *et al*. 2012; Rodríguez-Santiago *et al*. 2015), the Japanese population of *P. disjunctivus* may have become infected in aquaria in which other loricariids were kept. The fish species found in Okinawa-jima inland waters are the descendants of released ornamental pets originally held in aquaria (Takeshima and Yoshino 1996), and Shimadzu (2016) suggested that the sailfin catfish of this island had been hybridized with *Pterygoplichthys* spp. before importation. As a possibly relevant environmental factor, water temperature ranged from 24.0°C to 30.8°C at the sampling site in Campeche (Rodríguez-Santiago *et al*. 2015), but was lower, ranging from 16.3°C to 28.2°C in the Hija River on Okinawa-jima island (Shimadzu 2008). Possibly due to the high water temperature, monogeneans other than *H. heterotylus* might have not been able to become established in Campeche. No information on the native monogenean fauna of *P. disjunctivus* is available, and it is necessary to examine wild loricariids from South America and the temperature tolerance of these monogeneans.

To date, nine nominal and two undetermined species of dactylogyrid monogenean have been reported from seven species of freshwater fish in Okinawa Prefecture, and they were found only on non-native and/or cultured hosts: *Dactylogyrus extensus* Mueller and Van Cleave, 1932 from common carp *Cyprinus carpio* Linnaeus, 1758 (Cypriniformes: Cyprinidae) (Nitta and Nagasawa 2015c); *Dactylogyrus* sp./spp. from cultured koi carp *C. carpio* (Tamaki and Nakamura 2007a); *Cichlidogyrus sclerosus* Paperna and Thurston, 1969, *C. halli* (Price and Kirk, 1967), and *C. tilapiae* Paperna, 1960 from Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) and Mozambique tilapia *O. mossambicus* (Peters, 1852) (Perciformes: Cichlidae) (Maneepitaksanti and Nagasawa 2012b); *Salsuginus seculus* (Mizelle and Arcadi, 1945) from mosquitofish *Gambusia affinis* (Baird and Girard, 1853) (Cyprinodontiformes: Poeciliidae) (Nitta and Nagasawa 2014c); *Heteropriapulus heterotylus*, *Unilatus unilatus*, *U. brittani*, and *Trinigyrus peregrinus* from *P. disjunctivus* (Nitta and Nagasawa 2013, 2016c); and *Pseudodactylogyrus* sp./spp. from European eel *Anguilla anguilla* (Linnaeus, 1758) and Japanese eel *A. japonica* Temminck and Schlegel, 1846 (Anguilliformes: Anguillidae) imported from France and Taiwan, respectively (Inoha 1974) and from cultured *A. japonica* (Tamaki and Nakamura 2007b). About 300 species of fish are found in inland waters of Okinawa Prefecture (Nishida and Yoshino 2003), and they certainly harbor many native species of monogenean. Studies are needed of the monogenean fauna of the native freshwater fishes in this prefecture.

4.3 Alien Monogenean of the Mosquitofish *Gambusia affinis*

4.3.1 Introduction

The mosquitofish *Gambusia affinis* (Baird and Girard, 1853) are native to North America, ranging from New Jersey to southern Mexico (Rosen 1973). Since the 1900s, this species

has been transplanted to various countries and regions to control mosquitos, which has resulted in its pan-global spread, and now it is one of the most widely introduced freshwater fishes in the world (Welcomme 1988).

Mosquitofish were introduced from Taiwan into Japan in the late 1910s for control of mosquitos and malaria: they were brought to Nara, Tōkyō, and Okinawa prefectures in 1916, 1917, and 1919, respectively (Ida 1918; Matsui 1917; Kuroiwa 1927). Subsequently, mosquitofish were released at many locations in Japan and by 1979 they had become established in 25 prefectures (Wada 1979). In particular, mosquitofish were transplanted in 1968 from Tōkyō to Tokushima city, Tokushima Prefecture, where they were reproduced in tanks by the city government (Tashiro *et al.* 2007). In 1969 and afterwards, mosquitofish produced there were released into water bodies at various locations in Japan for the extermination of mosquitos and water clarification (Tashiro *et al.* 2007). They have thus become established in a wide area of Japan, ranging from Nagano Prefecture in central Honshū in north through Shikoku and Kyūshū to Iriomote Island, Okinawa Prefecture, in the south (Anonymous 2010b). The release program, however, was ended in 2005, when the species was designated by the national government as one of the most serious invasive alien species in Japan (Tashiro *et al.* 2007). Recently, I found the dactylogyrid monogenean *Salsuginus seculus* (Mizelle and Arcadi, 1945) on the gills of mosquitofish collected at five sites in Japan.

4.3.2 Results

Salsuginus seculus was found on the gills of mosquitofish collected at five of the six sites (Table 6). Prevalence and intensity varied between sampling sites, but prevalence was higher at sites 1–3 and 6 where the water was freshwater. The water taken at sites 4 and 5 was brackish. A few worms occurred at site 4, where salinity remained low, but no worms were found at site 5, where salinity was higher.

4.3.2.1 ***Salsuginus seculus*** (Mizelle and Arcadi, 1945)

(Fig. 14)

Urocleidus seculus Mizelle and Arcadi, 1945: 293–296, figs 1–20; Sproston 1946: 249, 525; Seamster 1948: 168; Mizelle *et al.* 1956: 174, 177; Yamaguti 1963: 83; Hoffman 1967: 93, 387; Nowlin *et al.* 1967: 111; Price 1968b: 191; Meade and Bedinger 1972: 285, fig. 32.

Salsuginus seculus: Murith and Beverley-Burton, 1985: 705, 712; Beverly-Burton and Klassen 1990: 5; Font 1997: 58; Hoffman 1999: 119; Aguilar-Aguilar *et al.* 2003: 1871; Aguilar-Aguilar *et al.* 2005: 238; Pineda-López *et al.* 2005: 441, 445; Ray 2005: 14; Salgado-Maldonado *et al.* 2005: 153, 156; Kohn *et al.* 2006: 35, 74; Salgado-Maldonado 2006: 165, 348; Salgado-Maldonado 2008: 39; Lee and Reusser 2012: 430–431; Zhang 2012: 103; Salgado-Maldonado and Quiroz-Martínez 2013: 5, 10, 12.

Material examined. Three specimens (NSMT-Pl 6127) from an irrigation canal flowing into Urauchi Bay, Okinawa Prefecture; 15 specimens (NSMT-Pl 6128) from an irrigation canal connected to the Ushitsu River, Saga Prefecture; 18 specimens (NMST-Pl 6129) from the middle reaches of the Umeda River, Aichi Prefecture; four specimens (NMST-Pl 6130) from an irrigation canal connected to the Yoshino River system, Tokushima Prefecture; three specimens (NMST-Pl 6141) from the Dōno River, Kyōto Prefecture, Japan.

Description. Body elongate in live, but greatly contracted upon fixation (Fig. 14A), 203±62.1 (129–354; *n*=36) long, 128±25.0 (71–178; *n*=35) wide. Three pairs of head organs. Usually one pair of eye-spots with some dissociated eyes, anterior pair present in some specimens. Alimentary system consisting of spherical pharynx (diameter 21±4.1 [17–33; *n*=39]), esophagus very short or not present, and bifurcate intestinal caeca unit posterior to testis. Testis posterior to ovary. Vas deferens looping dorsoventrally around left intestinal caecum, seminal vesicle expanded before entering base of penis. Two glandular prostatic reservoirs arranged behind of penis; dorsal one rounded, ventral one U-shaped. Sclerotized penis (Fig. 14G) slightly curved, 19±1.0 (18–21; *n*=23) in chord length from base to tip; 29±1.8 (27–32; *n*=23) in arc length along curve. Accessory piece (Fig. 14G) rod-like with distal projection, length 14±1.0 (12–16; *n*=22). Ovary elliptical, with oviduct arising from its anterior part. Vaginal armament unsclerotized, surrounded by thick membrane. Vaginal pore located at same level as penis on left body surface, vaginal duct arising from left side of oötype. Oviduct originating from anterior side of ovary, continues as oötype. Uterus extending anteriorly to uterine pore close to penis. Mehlis' gland connected to oötype. Vitellaria well developed, abundantly distributed around intestinal caeca.

Haptor length 35±7.9 (22–56; *n*=36), width 66±12.4 (46–103; *n*=36). Dorsal hamuli (Fig. 14B): total length 17±0.6 (16–18; *n*=13), length to notch 15±0.5 (15–16; *n*=13), deep root length 2±0.5 (1–2; *n*=13), superficial root length 7±0.9 (6–9; *n*=13), blade length 6±0.5 (5–6; *n*=13), curvature of blade 0.8±0.04 (0.7–0.8; *n*=13). Ventral hamuli (Fig. 14C): total length 19±1.0 (17–21; *n*=17), length to notch 17±1.0 (16–19; *n*=17), deep root length 2±0.5 (1–2; *n*=17), superficial root length 9±1.0 (7–10; *n*=17), blade length 6±0.4 (5–7; *n*=17), curvature of blade 0.9±0.1 (0.7–0.9; *n*=17). Dorsal bar (Fig. 14D): transverse length 23±1.6 (20–27; *n*=41), median width 3±0.6 (2–4; *n*=41); distal notch blunt or absent in some specimens. Ventral bar (Fig. 14E): transverse length 25±1.9 (21–29; *n*=39), median width 3±0.6 (2–4; n=39); distal notch sharp. Larval hooks in 7 pairs (Fig. 14F), all similar in shape and size; length 10±0.5 (10–11; *n*=42).

Host. Mosquitofish *Gambusia affinis* (Cyprinodontiformes: Poeciliidae).

Localities. An irrigation canal flowing into Urauchi Bay, Iriomote Island (the Ryūkyū Islands), Okinawa Prefecture; an irrigation canal connected to the Ushitsu River, Ashikari, Ogi city, Saga Prefecture; the Umeda River, Hamamichi, Toyohashi city, Aichi Prefecture; an irrigation canal connected to the Yoshino River system, Kawauchi, Tokushima city, Tokushima Prefecture; the Dōno River, Momoyama, Fushimi District, Kyōto city, Kyōto Prefecture.

Site of infection. Gill filaments.

Remarks. The present collection represents the first records of *S. seculus* from Japan. The species was originally described as *Urocleidus seculus* from *Gambusia affinis* (as *G. affinis affinis*) collected in California, U.S.A. (Mizelle and Arcadi 1945), and was later transferred to *Salsuginus* by Murith and Beverley-Burton (1985). The species has been reported from Mexico (Aguilar-Aguilar *et al.* 2003; Salgado-Maldonado *et al.* 2005) and Hawaii (Font 1997), in addition to the continental United States [California: Mizelle and Arcadi (1945); Louisiana: Seamster (1948); Texas: Nowlin *et al.* (1967), Meade and Bedinger (1972)].

The measurements and morphology of sclerotized parts of the specimens of *S. seculus* collected in the present study are almost identical to those of representatives of this species from California and Texas (Mizelle and Arcadi 1945; Meade and Bedinger 1972). The measurements of haptoral sclerotized parts of the specimens also agree with those of S. seculus reported by Rand and Wiles (1987), but the dorsal deep root and ventral blade of the present specimens (1–2 and 5–6 µm, respectively) are slightly shorter than those reported earlier (3 and 7 µm, respectively).

Twelve species of *Salsuginus* are currently recognized as valid (in alphabetical order): *S. angularis* (Mueller, 1934); *S. bahamianus* (Hanek and Fernando, 1972); *S.*

bermudae Rand and Wiles, 1987; *S. cubensis* Mendoza-Franco, Vidal-Martinez, Cruz-Quintana, and Leon, 2006; *S. fundulus* (Mizelle, 1940); *S. heterocliti* Murith and Beverley-Burton, 1985; *S. neotropicalis* Mendoza-Franco and Vidal-Martinez, 2001; *S. seculus* (Mizelle and Arcadi, 1945); *S. spirae* (Williams, 1980); *S. thalkeni* Janovy, Ruhnke, and Wheeler, 1989; *S. umbraensis* (Mizelle, 1938); and *S. yutanensis* Ferdig, McDowell, and Janovy, 1991. *Salsuginus seculus* differs from both *S. umbraensis* and *S. fundulus* which are characterized by the same size of the dorsal and ventral hamuli (Mizelle 1938, 1940; Beverley-Burton 1984; Murith and Beverley-Burton 1985). By the accessory piece length, *S. seculus* (12–16 µm: this study) is distinguished from *S. bahamianus* (27–34 µm: Hanek and Fernando 1972c), *S. heterocliti* (20–24 µm: Murith and Beverley-Burton 1985), and *S. spirae* (20–25 µm: Williams 1980; 19–20 µm: Murith and Beverley-Burton 1985). The accessory piece of *S. seculus* has one process, while those of *S. angularis*, *S. bermudae*, *S. cubensis*, and *S. heterocliti* possess multiple processes (Murith and Beverley-Burton 1985; Rand and Wiles 1987; Mendoza-Franco *et al*. 2006). *Salsuginus seculus* is also discerned from *S. neotropicalis* which has a ventral bar with enlarged globose ends (Mendoza-Franco and Vidal-Martínez 2001). The dorsal curvature of the blade in *S. seculus* (0.8: this study) is smaller than that in *S. thalkeni* (1.0: Janovy *et al*. 1989) and *S. yutanensis* (1.1: Ferdig *et al*. 1991).

Salsuginus seculus is the third species of parasites reported from the mosquitofish in Japan. To date, *Genarchopsis goppo* Ozaki, 1925 (Digenea: Derogenidae) and *Neoergasilus japonicus* (Harada, 1930) (Copepoda: Ergasilidae) have been recorded from the fish (Shimazu *et al*. 2011; Nagasawa and Uyeno 2012). These parasite are native to eastern Asia, (Shimazu 1995; Nagasawa and Uyeno 2012) and are not introduced species of North American origin.

4.3.3 **Discussion**

Based on the history of introduction of mosquitofish into Japan, it is most likely that *S. seculus* was brought along with the fish from Texas, U.S.A., through Hawaii and Taiwan to Japan. After firstly having been introduced from Texas into Hawaii in 1905 (Seale 1905), mosquitofish were transported from Hawaii to Taiwan in 1911 (Anonymous 1932) and thence to Japan in the late 1910s. While there is no record of *S. seculus* from Taiwan, this parasite may infect mosquitofish there. Furthermore, because mosquitofish have become established all over the world (Welcomme 1988), *S. seculus* might have gained a global distribution as well. The species has been reported from Hawaii (Font 1997) outside the natural range of mosquitofish (North America), but it has not yet been found in New Zealand despite intensive parasitological examination of mosquitofish

(Zhang 2012).

In all records (see synonymy for literature citations), *S. seculus* has been described from *G. affinis*. This monogenean most likely has a high host specificity for this fish. Hanek and Fernando (1972c) recorded *S. seculus* from mosquitofish in the Bahamas, where the present fish species is not distributed but two related species, *Gambusia manni* Hubbs, 1927 and *G. puncticulata* Poey, 1854 (as *G. hubbsi* Breder, 1934), occur (Böhlke and Chaplin 1968, 1993; Smith-Vaniz and Böhlke 1991). Thus, Hanek and Fernando (1972c) might have misidentified either or both of these fishes as mosquitofish. Furthermore, considering the host specificity of *S. seculus*, monogeneans parasitic on "mosquitofish" in the Bahamas are probably not *S. seculus* but other undescribed species.

There was a difference in the infection level of *S. seculus* on mosquitofish collected at the two sites near Tokushima city (Table 6). The monogenean occurred at site 4 where salinity was low but it was not found at site 5 with slightly higher salinity. This may indicate that this monogenean has a low salinity tolerance and can become establish only in quite low saline environments. According to Rand and Wiles (1987), no mosquitofish were infested with *S. seculus* in brackish-water lakes of Bermuda. It is desirable to investigate the occurrence of the species on mosquitofish in waters at various salinity levels.

Salsuginus bermudae was reported from mosquitofish in Guangdong, China (Xiong and Ding 2011) as an introduced species. This congener of *S. seculus* is a parasite of *Fundulus bermudae* Günther, 1874, which is endemic to Bermuda (Smith-Vaniz *et al.* 1999) and is known to infect mosquitofish, which were introduced into Bermuda in 1927 (Rand and Wiles 1987). While mosquitofish were transplanted into China in 1926 (Sowerby 1927; Hwang and Chow 1990) from Hawaii and the Philippines (Seale 1917), there is no record of their introduction from Bermuda into China. Considering this history of the introduction of mosquitofish and that *S. bermudae* morphologically resembles *S. seculus* (Rand and Wiles 1987), the monogeneans reported by Xiong and Ding (2011) from Chinese mosquitofish is not likely to be *S. bermudae* but *S. seculus*.

Chapter 5. General Discussion

In this study, 10 species of monogeneans belonging to Dactylogyridea were found from Japanese freshwater fishes. These monogeneans consist of six introduced species (one and five new to science and Japan, respectively) and four native species including one endemic species (one and three new to science and Japan, respectively). After this study, the number of dactylogyridean and alien monogenean species parasitic on freshwater fishes is increased each from 45 to 55 and 9 to 15 in Japan. So far, about 228 species of monogeneans have been reported from Japan (Table 1), but if a single species of monogenean occurs on a single species of fish, about 4,400 species of monogeneans are estimated to occur on Japanese fishes, because the same number of fishes are found in Japan (Nakabo 2013; Anonymous 2016). Based on my estimate (Nitta 2013, unpublished bachelor thesis), one species of Japanese freshwater fish harbors 1.3–1.8 species of monogeneans on average. About 500 species of freshwater fishes occur (Hosoya 2015b), and it is thus estimated that 650 to 900 species of monogeneans inhabit Japanese inland waters. Gyrodactylidae (mainly *Gyrodactylus*) and Dactylogyridae (mainly *Dactylogyrus* and *Ancyrocephalus* s. l.) are the major groups of monogeneans parasitic on freshwater fishes (*e.g.* Wu *et al*. 2000; Galli *et al*. 2010). So far, only 15 species of *Gyrodactylus* and 38 species of dactylogyrids have been described from native freshwater fishes in Japan, and many undescribed and unreported monogeneans are found to infect them (Nitta unpublished; Kazuo Ogawa, Meguro Parasitological Museum, pers. comm.).

In total, 76 nominal species of monogeneans have been recorded from freshwater fishes in Japan, but most of these species have been found from commercially important fishes from the viewpoint of fish diseases. In this country, about 90 endemic freshwater fish species occur (Biodiversity Center of Japan 2002), and monogeneans infecting those endemic fishes are also likely to be endemic. *Dactylogyrus bicorniculus* is one of the endemic parasites and most likely faces the danger of extinction with its host, *Rhodeus atremius atremius* (Section 3.2). The parasite fauna of the endangered fishes is poorly understood (Urabe 2010), and only 10 species of monogeneans have been reported from six species of those fishes (Section 3.1, 3.2). Co-extinction of parasites will be caused by extinction and sudden decrease of wild hosts and alteration of local ecosystems (Windsor 1990; Stork 1993; Baruš *et al.* 1997; Urabe 2010). In addition, healthy ecosystems have healthy parasite faunas, and parasites as indicators will show general environmental quality and ecosystem health (Marcogliese 2005; Poulin 2007). It is highly desirable to clarify the parasite fauna of the freshwater fishes on the verge of co-extinction and conserve biological diversity including parasitic species in Japan.

The Japanese Archipelago consists of about 6,800 islets, and the past parasitological surveys of freshwater fishes were conducted on the major islands, Honshū, Hokkaidō, Shikoku, and Kyūshū. Almost nothing is known about monogeneans of freshwater fishes on other numerous islands (Nagasawa *et al*. 2013). It is thus desirable to study the monogenean fauna of such islands and to compare it with that of the major islands in order to clarify the dispersion of monogeneans and environmental characteristics for the persistence of their populations. Especially, the monogenean fauna of brackish-water fishes is unclear (Table 1).

A total of 31 nominal species of monogeneans have so far been found from Okinawa Prefecture, the Ryūkyū Islands, southern Japan (Nitta unpublished). Subtropical fishes have been suggested to expand their distribution northward to the Japanese main islands with global warming (Kuwahara *et al*. 2006), and research on monogeneans should be more intensively conducted in southern Japan to monitor their distributional change. According to Hasegawa (2002), a small number of freshwater fishes have been examined for their parasites, and there is no study on the parasites of brackish-water fishes. As about 500 species of fishes occur in the inland waters of Okinawa Prefecture (Yoshigou 2014), more study is needed to clarify the monogenean fauna on the fresh and brackish-water fishes of this prefecture.

Eight species of monogeneans have been identified to the species level from freshwater fishes in Okinawa Prefecture, but all of them are alien species. The common carp *Cyprinus carpio* was transplanted to this prefecture before the 19th century (Kochi 2003), and one species of dactylogyrid, *Dactylogyrus extensus* is co-introduced with the fish (Nitta and Nagasawa 2015c). As new fisheries resources, Mozambique tilapia *Oreochromis mossambicus* and Nile tilapia *O. niloticus* were introduced into Okinawa Prefecture (Takehara *et al*. 1997) and accompanied three species of dactylogyrids (*i.e. Cichlidogyrus halli*, *C. sclerosus*, and *C. tilapiae*) (Maneepitaksanti and Nagasawa 2012b). Another dactylogyrid *Salsuginus seculus* was co-introduced with the mosquitofish *Gambusia affinis* transplanted to control mosquitos (Section 4.3). Four species of monogeneans native to Latin America, *Heteropriapulus heterotylus*, *Trinigyrus peregrinus*, *Unilatus brittani*, and *U. unilatus*, have been reported from the vermiculated sailfin catfish *Pterygoplichthys disjunctivus* in Okinawa Prefecture, which has been suggested as a result of co-introduction through the release of ornamental pet fish into the prefecture's inland waters (Section 4.2). About 20 species of ornamental fishes have been recorded from the inland waters of Okinawa-jima Island (Ishikawa *et al*. 2013) and it is most likely that ornamental fish trade is one of the major invasion routes of alien fish monogeneans to Okinawa Prefecture.

The monogeneans can establish more readily together with their hosts than other groups of parasites because of their simple life cycle (Bauer and Hoffman 1976), and, like *Salsuginus seculus*, can also colonize after passing through one or several other countries (Section 4.3). However, only one monogenean species, *Ligictaluridus pricei*, has been collected from channel cat fish which harbors 4 species in native habitat (Section 4.1; Hoffman 1999). In this study, only one specimen of the fish has been examined for their parasites. More study of monogeneans not successfully introduced with the fish host will clarify the requirements for establishing introduced species, and it is possible to establish a method for controlling alien parasites and their invasion.

Several reports have described high negative impacts of alien monogeneans on certain wild fishes, and dramatic decreases in wild fish stocks due to heavy and uncontrolled infections by introduced monogeneans are known (*e.g.* Petrushevski and Shulman 1970; Johnsen and Jensen 1986; Ogawa 2002; Yoshinaga *et al*. 2009). The fringebarbel sturgeon *Acipenser nudiventris* Lovetsky, 1828, was transported around 1930 from the Caspian Sea to the Aral Sea for naturalization, but in 1936 the co-introduced capsalid monogenean *Nitzschia sturionis* (Abildgaard, 1794) caused high mortality of the native fringebarbel sturgeon, and its stock became a very bad status (Petrushevski and Shulman 1970). Similarly, the gyrodactylid monogenean *Gyrodactylus salaris* Malmberg, 1957 has been introduced with the Atlantic salmon *Salmo salar* Linnaeus, 1758 into Norwegian rives from Sweden, and caused heavy damages in the Norwegian salmon stocks (Johnsen and Jensen 1986). Also, in Japan, the introduced monogenean *Neoheterobothrium hirame* Ogawa, 1999 induced a decline of wild bastard halibut *Paralichthys olivaceus* Temminck and Schlegel, 1846 (Ogawa 2002; Yoshinaga *et al*. 2009). There are several comprehensive studies on the monogenean fauna of introduced fishes in terms of dangerousness of alien parasites (*e.g.* Anonymous 2012; Davydov *et al*. 2012; Salgado-Maldonado and Rubio-Godoy 2014). Based on this and previous studies, 15 species of alien monogeneans have been reported from nine species of introduced freshwater fishes in Japan (Table 7). In Japan, about 50 fish species have been introduced from other countries (Matsuzawa and Senou 2008), and almost all the introduced live fishes are considered to bring foreign monogeneans to Japanese waters. Therefore, the equivalent or more number of species of monogeneans may have established in Japan. Moreover, no information is available about the parasites of Japanese domestic alien fishes. The risk of introduced monogeneans is poorly understood in Japan, and it is necessary to clarify the monogenean fauna of such domestic alien fishes to take necessary actions.

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Table. 1. Nominal species of monogeneans parasitic on fishes, amphibians, reptails and invertebrates in Japan. The higher classification of monogeneans follows Gibson and Artois (2015). The scientific names of hosts are recommended by Froese and Pauly (2016) and the Herpetological Society of Japan (2016), and Japanese names follow Nakabo (2013) and the Herpetological Society of Japan (2016). Collection water shows as S: sea water, B brackish water and F: fresh water.

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
Class Monogenea van Beneden, 1858							
Subclass Monopisthocotylea Odhner, 1912							
Order Monocotylidea Lebedev, 1988							
Family Monocotylidae Lebedev, 1988							
1. *Calicotyle mitsukurii* Goto, 1894		*Squatina*	*japonica*	カスザメ	cloaca	Goto (1894)	S
2. *Calicotyle japonica* Kitamura, Ogawa, Shimizu, Kurashima, Mano, Taniuchi and Hirose, 2010		*Squalus*	*mitsukurii*	フトツノザメ	uterus, rectal gland, cloaca	Kitamura *et al*. (2010)	S
3. *Dendromonocotyle akajeii* Ho and Perkins, 1980		*Dasyatis*	*akajei*	アカエイ	skin	Ho and Perkins (1980)	S
4. *Heterocotyle chinensis* Timofeeva, 1983		*Dasyatis*	*akajei*	アカエイ	gill	Nitta and Nagasawa (2015a)	S, B
5. *Monocotyle ijimae* Goto, 1894		*Dasyatis*	*akajei*	アカエイ	mouth cavity	Goto (1894)	S
Order Capsalidea Lebedev, 1988							
Family Capsalidae Baird, 1853							
6. *Allobedenenia convoluta* (Yamaguti, 1937) Yamaguti, 1963	*Epibdella* (*Benedenia*) *convoluta* Yamaguti, 1937	*Epinephelus*	*akaara*	キジハタ	gill	Yamaguti (1937b)	S
		Epinephelus	*septemfasciatus*	マハタ	gill	Iwata (1990a)	S
7. *Benedenia epinepheli* (Yamaguti, 1937) Meserve, 1938	*Epibdella* (*Epibdella*) *epinepheli* Yamaguti, 1937	*Epinephelus*	*akaara*	キジハタ	gill	Yamaguti (1937b)	S
	Benedeniella congeri Yamaguti, 1958	*Conger*	*myriaster*	マアナゴ	gill	Yamaguti (1958)	S
	Neobenedeniella congeri (Yamaguti, 1958)	*Aluterus*	*monoceros*	ウスバハギ	fins, eyes	Kamegai, Sh. *et al*. (1985)	S
		Balistoides	*conspicillus*	モンガラカワハギ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Chaetodon	*auriga*	トゲチョウチョウウオ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Diodon	*holocanthus*	ハリセンボン	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Epinephelus	*akaara*	キジハタ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Epinephelus	*bruneus*	クエ	fins, eyes, body surface	Tsutsui and Ito (1965), Ogawa *et al*. (1995a)	S
		Epinephelus	*septemfasciatus*	マハタ	fins, eyes, body surface	Ogawa *et al*. (1995a), Hanyu *et al*. (2009)	S
		Epinephelus	*suillus*	チャイロマルハタ	fins, eyes, body surface	Ogawa *et al*. (1995)	S
	Benedenia sp.	*Goniistius*	*zonatus*	タカノハダイ	fins, gills, body surface	Tsutsui and Ito (1965)	S
		Oplegnathus	*punctatus*	イシガキダイ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
	Benedenia sp.	*Ostracion*	*immaculatus*	ハコフグ	fins, eyes, body surface	Tsutsui and Ito (1965), Ogawa *et al*. (1995a)	S
		Ostracion	*cubicus*	ミナミハコフグ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Paralichthys	*olivaceus*	ヒラメ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Pterois	*volitans*	ハナミノカサゴ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
	Benedenia sp.	*Takifugu*	*niphobles*	クサフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Takifugu*	*pardalis*	ヒガンフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Takifugu*	*poecilonotus*	コモンフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Takifugu*	*porphyreus*	マフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Takifugu*	*radiatus*	ナシフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Takifugu*	*snyderi*	ショウサイフグ	fins, gills, body surface	Tsutsui and Ito (1965)	S
	Benedenia sp.	*Echeneis*	*naucrates*	コバンザメ	fins, gills, body surface	Tsutsui and Ito (1965)	S
		Sebastiscus	*marmoratus*	カサゴ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
		Sebastes	*schlegeli*	クロソイ	fins, eyes, body surface	Ogawa *et al*. (1995a)	S
	Benedenia sp.	*Semicossyphus*	*reticulatus*	コブダイ	fins, gills, body surface	Tsutsui and Ito (1965)	S
8. *Benedenia derzhavini* (Layman, 1930) Meserve, 1938		*Sebastes*	sp.	メバル属の一種	gill	Ho and Perkins (1980)	S
9. *Benedenia hoshinai* Ogawa, 1984	*Benedenia* sp.	*Oplegnathus*	*fasciatus*	イシダイ	fin, skin	Hoshina (1966b), Hatai (1983a), Hirakawa *et al*. (1984), Ogawa (1984a, c)	S
10. *Benedenia ishikawae* (Goto, 1894) Monticelli, 1902	*Epibdella ishikawae* Goto, 1894	*Lethrinus*	sp.	フエフキダイ属の一種	gill	Goto (1894)	S
11. *Benedenia elongata* (Yamaguti, 1968) Egorova, 1997	*Benedenia kintoki* Iwata, 1990	*Cookeolus*	*japonicus*	チカメキントキ	gill	Iwata (1990a)	S
12. *Benedenia ovata* (Goto, 1894) Johnston, 1929	*Epibdella ovata* Goto, 1894, *Benedenia akaisaki* Iwata, 1990	*Caprodon*	*schlegelii*	アカイサキ	gill	Goto (1894), Iwata (1990a)	S
13. *Benedenia sekii* (Yamaguti, 1937) Meserve, 1938	*Epibdella* (*Epibdella*) *sekii* Yamaguti, 1937	*Pagrus*	*major*	マダイ	body surface	Yamaguti (1937b), Yasunaga (1981)	S
14. *Benedenia seriolae* (Yamaguti, 1934) Price, 1939	*Epibdella seriolae* Yamaguti, 1934	*Seriola*	*lalandi*	ヒラマサ	gill	Yamaguti (1934), Iwata (1990a)	S
		Cantherhines	*pardalis*	アミメウマヅラハギ	-	Dyer *et al*. (1989)	S
	Epibdella seriolae Yamaguti, 1933	*Etelis*	*coruscans*	ハマダイ	gill	Kihara (1960)	S
		Seriola	*dumerili*	カンパチ	skin	Harada (1965b)	S
		Seriola	*quinqueradiata*	ブリ	skin	*e.g.* Hoshina (1964), Hoshina and Matsusato (1967b), Kasahara (1967a, b), Anonymous (1962)	S
		Seriola	*quinqueradiata* X *lalandi*	ブリ×ヒラマサ	skin	Nagakura *et al.* (2010)	S
15. *Benedenia synagrls* Yamaguti, 1953		*Arothron*	*mappa*	ケショウフグ		Dyer *et al*. (1989)	S
16. *Capsala biparasitica* (Goto, 1894) Price, 1938	*Tristomum biparasiticum* Goto, 1894	*Parapetalus*	sp.		Carapace	Goto (1894)	S
17. *Capsala foliacea* (Goto, 1894) Price, 1938	*Tristomum foliacea* Goto, 1894	undetermined species of fish			gill	Goto (1894)	S
18. *Capsala magronum* (Ishii, 1936) Price, 1938	*Tristoma magronum* Ishii, 1936	*Thunnus*	*orientalis*	クロマグロ	gill	Ishii (1936)	S
19. *Capsala martinieri* Bosc, 1811		*Mola*	*mola*	マンボウ	skin	Anonymous (1966a)	S
20. *Capsala notosinense* (Mamaev, 1968) Chisholm and Whittington, 2007	*Capsala katuo* Iwata, 1990	*Katsuwonus*	*pelamis*	カツオ	gill	Iwata (1990a)	S
21. *Capsala nozawae* (Goto, 1894) Price, 1938	*Tristomum nozawae* Goto, 1894	*Thunnus*	*obesus*	メバチ	fin	Goto (1894)	S
22. *Capsala katsuwoni* (Ishii, 1936) Price, 1938	*Tristoma katsuwonum* Ishii, 1936	*Katsuwonus*	*pelamis*	カツオ	gill	Ishii (1936)	S

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
23. *Capsala ovalis* (Goto, 1894) Price, 1938	*Tristomum ovale* Goto, 1894	*Istiophorus*	*platypterus*	バショウカジキ	month cavity	Goto (1894)	S
	Tristomum ovale Goto, 1894	*Kajikia*	*audax*	マカジキ	month cavity	Goto (1894)	S
	Tristomum ovale Goto, 1894	*Acanthocybium*	*solandri*	カマスサワラ	month cavity	Goto (1894), Ho and Perkins (1980)	S
		Istiophorus	*platypterus*	バショウカジキ	skin	Ho and Perkins (1980)	S
24. *Capsaloides sinuatus* (Goto, 1894) Price, 1938	*Tristomum sinuatus* Goto, 1894	*Kajikia*	*audax*	マカジキ	gill-plates	Goto (1894)	S
25. *Encotyllabe spari* Yamaguti, 1934		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Yamaguti (1934)	S
		Diagramma	*pictum*	コロダイ	gill	Yamaguti (1934)	S
		Epinephelus	*akaara*	キジハタ	gill	Yamaguti (1934)	S
		Lethrinus	*nebulosus*	ハマフエフキ	gill	Iwata (1990b)	S
		Plectorhynchus	pictus	コロダイ	gill	Iwata (1990b)	S
		Upeneus	*tragula*	ヨメヒメジ	gill	Iwata (1990b)	S
		Nemipterus	*virgatus*	イトヨリダイ	gill	Iwata (1990a)	S
		Pagrus	*major*	マダイ	gill	Iwata (1990a)	S
		Sebastis	sp.	メバル属の一種	gill	Iwata (1990a)	S
		Parapristipoma	*trilineatum*	イサキ	gill	Iwata (1990a)	S
26. *Enoplocotyle kidokoi* Kearn, 1993		*Gymnothorax*	*kidako*	ウツボ	skin	Kearn (1993)	S
27. *Entobdella squamula* (Heath, 1902) Johnston, 1929		*Taeniura*	*meyeni*	マダラエイ	skin	Dyer *et al*. (1989)	S
28. *Megalobenedenia derzhavini* (Layman, 1930) Egorova, 1994	*Benedenia derzhavini* (Layman, 1930)	*Sebastes*	*oblongus*	タケノコメバル	gill	Machida *et al*. (1972)	S
29. *Menziesia sebastodis* (Yamaguti, 1934) Whittington, Deveney and Wyborn, 2001	*Epibdella sebastodis* Yamaguti, 1934	*Sebastis*	sp.	メバル属の一種	gill	Yamaguti (1934)	S
	Epibdella sebastodis Yamaguti, 1934	*Etelis*	*coruscans*	ハマダイ	gill	Kihara (1960)	S
	Epibdella sebastodis Yamaguti, 1934	*Epinephelus*	*rivulatus*	クエ	gill	Kihara (1960)	S
	Benedenia sebastodis (Yamaguti, 1934)	*Sebastes*	sp.	メバル属の一種	gill	Iwata (1990a)	S
30. *Metabenedeniella hoplognathi* (Yamaguti, 1942) Yamaguti, 1963	*Metabenedeniella hoplognathi* Yamaguti, 1958, *Benedenia*	*Oplegnathus*	*fasciatus*	イシダイ	gill, body surface	Yamaguti (1958), Abe (1969)	S
	Metabenedeniella hoplognathi Yamaguti, 1958	*Epinephelus*	*septemfasciatus*	マハタ	gill	Yamaguti (1958)	S
		Oplegnathus	*fasciatus*	イシダイ	gill	Ho and Perkins (1980)	S
	Epibdella (*Benedenia*) *hoplognathi* Yamaguti, 1942	*Oplegnathus*	*punctatus*	イシガキダイ	gill	Yamaguti (1942)	S
		Plectorhinchus	*chaetodonoides*	チョウチョウコショウダイ	-	Dyer *et al*. (1989)	S
	Benedenia hoplognathi Yamaguti, 1942	*Oplegnathus*	*punctatus*	イシガキダイ	gill	Iwata (1990a)	S
31. *Neobenedenia melleni* (MacCallum, 1927) Yamaguti, 1963	*Neobenedenia girellae* (Hargis, 1955) Yamaguti, 1963	*Epinephelus*	*akaara*	キジハタ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Epinephelus*	*cyanopodus*	ツチホゼリ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Epinephelus*	*malabaricus*	ヤイトハタ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Epinephelus*	*septemfasciatus*	マハタ	body surface	Hanyu *et al*. (2009)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Epinephelus*	*suillus*	チャイロマルハタ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Lateolabrax*	*japonicus*	スズキ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Paralichthys*	*olivaceus*	ヒラメ	body surface	*e.g.* Bondad-Reantaso *et al*. (1995b), Ogawa *et al*. (1995b), Shirakashi *et al*. (2010, 2013)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Plectropomus*	*leopardus*	スジアラ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Pseudocaranx*	*dentex*	シマアジ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Seriola*	*dumerili*	カンパチ	body surface	*e.g.* Bondad-Reantaso *et al*. (1995a), Ogawa *et al*. (1995b), Shirakashi *et al*. (2013)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Seriola*	*lalandi*	ヒラマサ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Seriola*	*rivoliana*	ヒレナガカンパチ	body surface	Ogawa *et al*. (1995b), Bondad-Reantaso *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Scomber*	*japonicus*	マサバ	body surface	Yamamoto *et al*. (2006)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Takifugu*	*rubripes*	トラフグ	body surface	Ogawa *et al*. (1995b)	S
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Tilapia*	*nilotica*	ナイルティラピア	body surface	Ogawa *et al*. (1995b)	B?
	Neobenedenia girellae (Hargis, 1955) Yamaguti, 1963	*Verasper*	*variegatus*	ホシガレイ	body surface	*e.g.* Umeda and Hirazawa (2004), Hirazaw et al. (2004)	S
32. *Trilobiodiscus lutiani* Bychowsky and Nagibina, 1967		*Lutjanus*	*argentimaculatus*	ゴマフエダイ	gills	Iwata (1990b)	S
33. *Tristoma integrum* Diesing, 1850	*Tristomum rotundum* Goto, 1894	*Xiphias*	*gladius*	メカジキ	gill	Goto (1894)	S
34. *Tristoma laevis* (Verrill, 1875) Guiart, 1938		*Istiompax*	*indica*	シロカジキ	skin	Kido *et al*. (2016)	S
35. *Trochopus goniistii* Yamaguti, 1940		*Cheilodactylus*	*zonatus*	タカノハダイ	gill	Yamaguti (1940a)	S
36. *Trochopus hobo* Yamaguti, 1942		*Chelidonichthys*	*spinosus*	ホウボウ	gill	Yamaguti (1942)	S
Order Gyrodactylidea Bychowsky, 1937							
Family Gyrodactylidae van Beneden and Hesse, 1863							
37. *Gyrodactylus anguillae* Ergens, 1960		*Anguilla*	*anguila*	ヨーロッパウナギ	gill	Ogawa and Egusa (1980a)	F
38. *Gyrodactylus egusai* Ogawa and Hioki, 1986		*Anguilla*	*japonica*	ニホンウナギ	Skin	Ogawa and Hioki (1986)	F
39. *Gyrodactylus japonicus* Kikuchi, 1929		*Plecoglossus*	*altivelis*	アユ	skin, gill	Kikuchi (1929), Ogawa and Egusa (1978c), Inada *et al*. (1990), Timoshkin *et al*. (2011)	F
40. *Gyrodactylus kherulensis* Ergens, 1974		*Cyprinus*	*carpio*	コイ	fin, gill filament	Ogawa and Egusa (1978c), Ogawa (1994b), Timoshkin *et al*. (2011)	F
41. *Gyrodactylus kobayashii* Hukuda, 1940	*Gyrodactylus elegans* von Nordmann, 1832	*Carassius*	sp.	フナ類	skin	Yamaguti (1940a)	F
	Gyrodactylus elegans von Nordmann, 1832	*Carassius*	*gibelio*	キンギョ	skin	Yamaguti (1940a)	F
		Carassius	*gibelio*	キンギョ	fin, skin	Ergens and Ogawa (1978)	F
		Carassius	sp.	キンブナ	fin	Ogawa (1994b)	F
		-	-	-	-	Timoshkin *et al*. (2011)	F

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
42. *Gyrodactylus longoacuminatus* Žitňan, 1964		*Carassius*	*langsdorfii*	ギンブナ	fin	Ogawa (1994b), Timoshkin *et al* . (2011)	F
43. *Gyrodactylus masu* Ogawa, 1986		*Oncorhynchus*	*masou*	ヤマメ	skin, gill filaments, gill arch	Ogawa (1986b)	F
		Oncorhynchus	*masou ishikawae*	アマゴ	skin, gill filaments, gill arch	Ogawa (1986b)	F
		Oncorhynchus	*mykiss*	ニジマス	skin, gill filaments, gill arch	Ogawa (1986b)	F
		Oncorhynchus	*nerka*	ベニザケ	fin, gill	Ogawa (1994b)	F
44. *Gyrodactylus micracanthus* Hukuda, 1940		*Misgurnus*	*anguillicaudatus*	ドジョウ	fin	Ogawa (1994b)	F
45. *Gyrodactylus nipponensis* Ogawa and Egusa, 1978		*Anguilla*	*japonica*	ニホンウナギ	gill filament, gill arch	Ogawa and Egusa (1978c, 1980a), Hayward et al. (2001)	F
		Anguilla	*anguila*	ヨーロッパウナギ	gill	Ogawa and Egusa (1980a)	F
46. *Gyrodactylus pardalidis* Ogawa and Inoue, 1997		*Takifugu*	*paradalis*	ヒガンフグ	fin	Ogawa and Inoue (1997a)	S
47. *Gyrodactylus plecoglossi* Ogawa and Egusa, 1978		*Plecoglossus*	*altivelis*	アユ	fin	Ogawa and Egusa (1978c), Timoshkin *et al* . (2011)	F
48. *Gyrodactylus rubripedis* Ogawa and Inoue, 1997		*Takifugu*	*rubripes*	トラフグ	fin, skin	Ogawa and Inoue (1997a)	S
49. *Gyrodactylus sprostonae* Ling, 1962		*Cyprinus*	*carpio*	コイ	gill filament	Ogawa and Egusa (1978c)	F
	Gyrodactylus spirostomae Ling, 1962	-	-	-	-	Timoshkin *et al* . (2011)	F
50. *Gyrodactylus stankovici* Ergens, 1970		-	-	-	-	Timoshkin *et al* . (2011)	F
51. *Gyrodactylus tominagai* Ogawa and Egusa, 1978		*Plecoglossus*	*altivelis*	アユ	fin	Ogawa and Egusa (1978c), Timoshkin *et al* . (2011)	F
Family Anoplodiscidae Tagliani, 1912							
52. *Anoplodiscus spari* (Yamaguti, 1958) Ogawa and Egusa, 1981	*Pseudomicrobothrium spari* Yamaguti, 1958	*Acanthopagrus*	*schlegelii*	クロダイ	gill, fins	Yamaguti (1958), Ogawa and Egusa (1981b), Nitta and Nagasawa (2015d)	S
53. *Anoplodiscus tai* Ogawa, 1994		*Pagrus*	*major*	マダイ	fins	Ogawa (1994a)	S
Family Udonellidae Taschenberg, 1879							
54. *Udonella fugu* Freeman and Ogawa, 2010	*Udonella caligorum* Johnston, 1835	*Takifugu*	*rubripes*	トラフグ	argulidae	Yamaguti (1958)	S
	Udonella caligorum Johnston, 1835	Argulidae	-	チョウ科の一種	dorsal surface of the	Yamaguti (1958)	S
		Caligus	*fugu*	セトウオジラミ	body surface	Freeman and Ogawa (2010), Okawachi *et al* . (2012)	S
		Takifugu	*niphobles*	クサフグ	*Caligus fugu*	Freeman and Ogawa (2010), Okawachi *et al* . (2012)	S
		Takifugu	*niphobles*	クサフグ	*Caligus fugu*	Okawachi *et al* . (2012)	S
Family Tetraonchoididae Bychowsky, 1957							
55. *Heteropavlovskioides synodontis* Machida, 1978		*Trachinocephalus*	*myops*	オキエソ		Machida (1978)	S
		Saurida	*elongata*	トカゲエソ		Machida (1978)	S
56. *Pavlovskioides litoralis* Bychowsky, Gussev and Nagibina, 1965		*Trachinocephalus*	*myops*	オキエソ		Machida (1978)	S
		Saurida	*elongata*	トカゲエソ		Machida (1978)	S
Order Dactylogyridea Bychowsky, 1937							
Family Dactylogyridae Bychowsky, 1933							
57. *Bivaginogyrus obscurus* (Gussev, 1955) Gussev and Gerasev, 1985		*Pseudorasbora*	*pumila*	シナイモツゴ	gill	Nitta and Nagasawa (2014b)	F
		Pseudorasbora	*parva*	モツゴ	gill	Nitta and Nagasawa (2014b, 2016a)	F
58. *Dactylogyrus arcuatus* Yamaguti, 1942		*Carassius*	sp.	フナ類の一種	gill	Yamaguti (1942)	F
		Carassius	spp.	フナ類	-	Timoshkin *et al* . (2011)	F
59. *Dactylogyrus anchoratus* (Dujardin, 1845) Wagener, 1857		*Carassius*	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
		Cyprinus	*carpio*	コイ	gill	Ogawa and Egusa (1979a)	F
		Carassius	spp.	フナ類	-	Timoshkin *et al* . (2011)	F
60. *Dactylogyrus baueri* Gussev, 1955		*Carassius*	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al* . (2011)	F
61. *Dactylogyrus bicorniculus* Nitta and Nagasawa, 2016		*Rhodeus*	*atremius*	カゼトゲタナゴ	gill	Nitta and Nagasawa (2016b)	F
62. *Dactylogyrus biwaensis* Ogawa and Egusa, 1982		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1982)	F
63. *Dactylogyrus dulkeiti* Bychowsky, 1936		*Carassius*	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
64. *Dactylogyrus extensus* Mueller and Van Cleave, 1932		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1979b), Imada *et al* . (1976), Nakatsugawa and Muroga (1977), Nitta and Nagasawa (2015c)	F
65. *Dactylogyrus falciformis* Achmerow, 1952		*Cyprinus*	*carpio*	コイ	gill	Ogawa (1994b)	
66. *Dactylogyrus formosus* Kulwieć, 1927		*Carassius*	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
67. *Dactylogyrus gotoi* Gussev, 1963		*Lateolabrax*	*japonicus*	スズキ	gill	Nitta and Nagasawa (2014a, 2015d)	S, B
68. *Dactylogyrus intermedius* Wegener, 1909		*Carassius*	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al* . (2011)	F
69. *Dactylogyrus inversus* Goto and Kikuchi, 1917	*Microncotretna lateolabracis* Yamaguti, 1958	*Lateolabrax*	*japonicus*	スズキ	gill	Goto and Kikuchi (1917), Yamaguti (1938, 1958), Kamegai, Sh. (1981), Nitta and Nagasawa (2014a)	S, B
70. *Dactylogyrus kikuchii* Gussev, 1963		*Lateolabrax*	*japonicus*	スズキ	gill	Nitta and Nagasawa (2014a)	B
71. *Dactylogyrus kurenkowi* Gussev, 1955		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al* . (2011)	F

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
72. *Dactylogyrus magnihamatus* Achmerow, 1952		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
73. *Dactylogyrus minutus* Kulwieć, 1927		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1977a, 1982), Nakatsugawa and Muroga (1977)	F
74. *Dactylogyrus mrazeki* Ergens and Dulmaa, 1968		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1982)	F
75. *Dactylogyrus navicularis* Gussev, 1955		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
76. *Dactylogyrus primarius* Gussev, 1955		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
77. *Dactylogyrus pseudogobii* Achmerow, 1952		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
78. *Dactylogyrus rostrum* (?) Gussev, 1955		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
79. *Dactylogyrus sahuensis* Ling, 1973		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1982)	F
80. *Dactylogyrus securiformis* Gussev, 1955		Cyprinidae	sp.	コイ科の一種	-	Timoshkin *et al*. (2011)	F
81. *Dactylogyrus spiralis* Yamaguti, 1942		*Carassius*	sp.	フナ類の一種	gill	Yamaguti (1942)	F
		Carassius	spp.	フナ類	-	Timoshkin *et al*. (2011)	F
82. *Dactylogyrus squameus* Gussev, 1955		*Pseudorasbora*	*parva*	モツゴ	gill	Nitta and Nagasawa (2016a)	F
83. *Dactylogyrus takahashii* Ogawa and Egusa, 1982		*Cyprinus*	*carpio*	コイ	gill	Ogawa and Egusa (1982)	F
84 *Dactylogyrus vastator* Nybelin, 1924		*Carassius*	sp.	フナ類の一種	gill	Yamaguti (1940a)	F
		Carassius	*gibelio*	キンギョ	gill	Ogawa and Egusa (1979a)	F
		Carassius	spp.	フナ類	-	Timoshkin *et al*. (2011)	F
Family Ancylocephalidae (sensu lato) Bychowsky and Nagibina, 1968							
85. *Actinocleidus fergusoni* Mizelle, 1938		*Lepomis*	*macrochirus*	ブルーギル	gill	Grygier and Urabe (2003), Maneepitaksanti and Nagasawa (2012a)	F
86. *Ancyrocephaloides triacanthi* Yamaguti, 1938		*Triacanthus*	*biaculeatus*	ギマ	gill	Yamaguti (1938)	S
87. *Ancyrocephalus cruciatus* (Wedi, 1857) Lühe, 1909		*Misgurnus*	*anguillicaudatus*	ドジョウ	gill	Ogawa (1994b)	F
88. *Ancyrocephalus mogurndae* (Yamaguti, 1940) Gussev, 1955	*Haliotrema mogurndae* Yamaguti, 1940	*Odontobutis*	*obscura*	ドンコ	gill	Yamaguti (1940a)	F
	Haliotrema mogurndae Yamaguti, 1940	*Gymnogobius*	*urotaenia*	ウキゴリ	gill	Yamaguti (1940a)	F
		-	-	-	-	Timoshkin *et al*. (2011)	F
89. *Ancyrocephalus pseudorasborae* Achmerow, 1952		*Pseudorasbora*	*parva*	モツゴ	gill	Nitta and Nagasawa (2016a)	F
90. *Ancyrocephalus skrjabini* Gussev, 1955		-	-	-	-	Timoshkin *et al*. (2011)	F
91. *Ancylodiscoides parasiluri* Yamaguti, 1937		*Silurus*	*asotus*	ナマズ	gill	Yamaguti (1937b)	F
		Silurus	spp.	ナマズ類	-	Timoshkin *et al*. (2011)	F
92. *Bychowskyella pseudobagri* Achmerow, 1952		-	-	-	-	Timoshkin *et al*. (2011)	F
93. *Cichlidogyrus halli* (Price and Kirk, 1967) Paperna, 1979.		*Oreochromis*	*niloticus*	ナイルティラピア	gill	Maneepitaksanti and Nagasawa (2012b)	F
		Oreochromis	*mossambicus*	カワスズメ	gill	Maneepitaksanti and Nagasawa (2012b)	F
94. *Cichlidogyrus sclerosus* Paperna and Thurston, 1969		*Oreochromis*	*niloticus*	ナイルティラピア	gill	Maneepitaksanti and Nagasawa (2012b)	F
		Oreochromis	*mossambicus*	カワスズメ	gill	Maneepitaksanti and Nagasawa (2012b)	F
95. *Cichlidogyrus tilapiae* Paperna, 1960		*Oreochromis*	*niloticus*	ナイルティラピア	gill	Maneepitaksanti and Nagasawa (2012b)	F
96. *Haliotrema alatum* Yamaguti, 1942		*Parupeneus*	*cyclostomus*	マルクチヒメジ	gill	Yamaguti (1942)	S
		Parupeneus	*multifasciatus*	オジサン	gill	Yamaguti (1942)	S
		Acanthurus	*bariene*	カンランハギ	-	Dyer *et al*. (1989)	S
97. *Haliotrema crymanum* Klassen, 1993		*Ostracion*	*cubicus*	ミナミハコフグ	gill	Klassen (1993b)	S
98. *Haliotrema hatampo* Machida and Araki, 1977		*Pempheris*	*xanthoptera*	ミナミハタンポ	gill	Machida and Araki (1977)	S
99. *Haliotrema japonense* Yamaguti, 1934		*Parupeneus*	*chrysopleuron*	ウミヒゴイ	gill	Yamaguti (1934)	S
		Zanclus	*cornutus*	ツノダシ	-	Dyer *et al*. (1989)	S
100. *Haliotrema kurodai* Ogawa and Egusa, 1978		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Ogawa and Egusa (1978d)	S
101. *Haliotrema kusafugu* Klassen, 1993		*Takifugu*	*niphobles*	クサフグ	gill	Klassen (1993a)	S
102. *Haliotrema ornatum* Yamaguti, 1942		Unidentified fish of Apogonidae		テンジクダイ科の一種	gill	Yamaguti (1942)	S
103. *Haliotrema recurvatum* Yamaguti, 1942		*Parupeneus*	*cyclostomus*	マルクチヒメジ	gill	Yamaguti (1942)	S
104. *Haliotrema spinicirrus* (Yamaguti, 1953) Bychowsky and Nagibina, 1970	*Ancyrocephalus spinicirrus* Yamaguti, 1953	*Variola*	*albimarginata*	オジロバラハタ	-	Dyer *et al*. (1989)	S
105. *Haliotrema xesuri* Yamaguti, 1940		*Prionurus*	*scalprum*	ニザダイ	gill	Yamaguti (1940a)	S
106. *Heteropriapulus heterotylus* (Jogunoori, Kritsky and Venkatanarasaiah, 2004) Kritsky, 2007		*Pterygoplichthys*	*disjunctivus*	マダラロリカリア	gill	Nitta and Nagasawa (2013, 2016c)	F
107. *Lethrinitrema lethrini* (Yamaguti, 1937) Lim and Justine, 2011	*Ancyrocephalus lethrini* Yamaguti, 1937	*Lethrinus*	*haernatopterus*	フエフキダイ	gill	Yamaguti (1937b)	S
108. *Ligictaluridus pricei* (Mueller, 1936) Beverley-Burton, 1984		*Ictalurus*	*punctatus*	チャネルキャットフィッシュ	gill	Nitta and Nagasawa (2015b)	F
109. *Nasoancyrocephalus diorchis* Machida, 1979		*Naso*	*unicornis*	テングハギ		Machida (1979)	S
110. *Onchocleidus dispar* Mueller, 1936		*Lepomis*	*macrochirus*	ブルーギル	gill	Maneepitaksanti and Nagasawa (2013)	F
111. *Onchocleidus ferox* (Mueller, 1934) Mueller, 1936	*Urocleidus ferox* Mueller, 1934	*Lepomis*	*macrochirus*	ブルーギル	gill	Muroga *et al*. (1980)	F
		Lepomis	*macrochirus*	ブルーギル	gill	Grygier and Urabe (2003), Maneepitaksanti and Nagasawa (2012a)	F
		Lepomis	*macrochirus*	ブルーギル	-	Timoshkin *et al*. (2011)	F
112. *Onchocleidus furcatus* (Mueller, 1937) Wheeler and Beverley-Burton, 1989	*Haplocleidus furcatus* Mueller, 1937	*Micropterus*	*salmoides*	オオクチバス	-	Grygier and Urabe (2003), Timoshkin *et al*. (2011)	F
113. *Parancylocephaloides daicoci* Yamaguti, 1938		*Daicocus*	*peterseni*	ホシセミホウボウ	gill	Yamaguti (1938), Ho and Perkins (1980)	S
114. *Protancyrocephalus strelkowi* Bychowsky, 1957		*Dactyloptena*	*orientalis*	セミホウボウ	-	Dyer *et al*. (1989)	S
115. *Pseudamphibdella paralichthydis* Yamaguti, 1958		*Paralichthys*	*olivaceus*	ヒラメ	gill	Yamaguti (1958)	S
116. *Pseudancylodiscoides gigi* (Yamaguti, 1942) Yamaguti, 1963	*Ancylodiscoides gigi* Yamaguti, 1942	*Tachysurus*	*nudiceps*	ギギ	gill	Yamaguti (1942)	F
		-	-	-	-	Timoshkin *et al*. (2011)	F
117. *Pseudodactylogyroides apogonis* (Yamaguti, 1940) Ogawa, 1986	*Dactylogyrus apogonis* Yamaguti, 1940	*Apogon*	*semilineatus*	ネンブツダイ	gill	Yamaguti (1940a), Ogawa (1986a)	S

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
118. *Pseudohaliotrema sphincteroporus* Yamaguti, 1953		*Acanthurus*	*lineatus*	ニジハギ	-	Dyer *et al*. (1989)	S
		Acanthurus	*olivaceus*	モンツキハギ	-	Dyer *et al*. (1989)	S
		Cephalopholis	*urodeta*	ニジハタ	-	Dyer *et al*. (1989)	S
		Gerres	*oyena*	ミナミクロサギ	-	Dyer *et al*. (1989)	S
		Heniochus	*chrysostomus*	オニハタタテダイ	-	Dyer *et al*. (1989)	S
119. *Pseudohaliotrema thysanophrydis* (Yamaguti, 1937) Young, 1968	*Ancyrocephalus thysanophrydis* Yamaguti, 1937	*Inegocia*	*japonica*	トカゲゴチ	gill	Yamaguti (1937b)	S
120. *Salsuginus seculus* (Mizelle and Arcadi, 1945) Murith and Beverley-Burton, 1985		*Gambusia*	*affinis*	カダヤシ	gill	Nitta and Nagasawa (2014c)	S, B
121. *Syncleithrium fusiformis* (Mueller, 1934) Price, 1967	*Actinocleidus* sp., similar to *A. fusiformis* (Mueller, 1934) Mueller, 1937	*Micropterus*	*salmoides*	オオクチバス	gill	Grygier and Urabe (2003), Timoshkin *et al*. (2011)	F
122. *Thaparocleidus asoti* (Yamaguti, 1937) Lim, 1996	*Ancylodiscoides asoti* Yamaguti, 1937	*Silurus*	*asotus*	ナマズ	gill	Yamaguti (1937b)	F
	Ancyclodiscoides asoti (?) Yamaguti, 1937	*Silurus*	spp.	ナマズ類	-	Timoshkin *et al*. (2011)	F
123. *Thaparocleidus hamatovagina* (Yamaguti, 1942) Lim, 1996	*Ancylodiscoides hamatovagina* Yamaguti, 1942	*Silurus*	*asotus*	ナマズ	gill	Yamaguti (1942)	F
	Ancylodiscoides hamatovagina (?) Yamaguti, 1942	*Silurus*	spp.	ナマズ類	-	Timoshkin *et al*. (2011)	F
124. *Thaparocleidus infundibulovagina* (Yamaguti, 1942) Lim, 1996	*Ancylodiscoides infundibulovagina* Yamaguti, 1942	*Silurus*	*asotus*	ナマズ	gill	Yamaguti (1942)	F
125. *Thaparocleidus sigmoidovagina* (Yamaguti, 1942) Lim, 1996	*Ancylodiscoides sigmoidovagina* Yamaguti, 1942	*Silurus*	*asotus*	ナマズ	gill	Yamaguti (1942)	F
126. *Tetrancistrum nasonis* Young, 1967	*Pseudancyrocephalus duplicatus* Yamaguti, 1968	*Naso*	*unicornis*	テングハギ	gill	Machida (1979)	S
127. *Tetrancistrum sigani* Goto and Kikuchi, 1917		*Siganus*	*fuscescens*	アイゴ	gill	Goto and Kikuchi (1917), Yamaguti (1938)	S
128. *Trinigyrus peregrinus* Nitta and Nagasawa, 2016		*Pterygoplichthys*	*disjunctivus*	マダラロリカリア	gill	Nitta and Nagasawa (2016c)	F
129. *Unilatus brittani* Mizelle, Kritsky and Crane, 1968		*Pterygoplichthys*	*disjunctivus*	マダラロリカリア	gill	Nitta and Nagasawa (2016c)	F
130. *Unilatus unilatus* Mizelle and Kritsky, 1967		*Pterygoplichthys*	*disjunctivus*	マダラロリカリア	gill	Nitta and Nagasawa (2016c)	F
Family Calceostomatidae Parona and Perugia, 1890							
131. *Pseudocalceostoma sciaenae* (Yamaguti, 1940) Yamaguti, 1963	*Calceostoma sciaenae* Yamaguti, 1940	*Pennahia*	*argentata*	シログチ	gill	Yamaguti (1940a), Ichihara (1972)	S
Family Pseudodactylogyridae Ogawa, 1986							
132. *Pseudodactylogyrus anguillae* (Yin and Sproston, 1948) Gussev, 1965	*Pseudodactylogyrus microrchis* Ogawa and Egusa, 1976	*Anguilla*	*anguilla*	ヨーロッパウナギ	gill	Ogawa and Egusa (1976), Imada and Muroga (1977), Ogawa *et al*. (1985), Iwasita *et al*. (2002), Umeda *et al*. (2006)	F
		Anguilla	*japonica*	ニホンウナギ	gill	Ogawa *et al*. (1985), Horiuchi *et al*. (1988), Katahira *et al*. (2012)	F, B
		Anguilla	*marmorata*	オオウナギ	gill	Katahira and Nagasawa (2014)	F
		-	-	-	-	Timoshkin *et al*. (2011)	F
133. *Pseudodactylogyrus bini* (Kikuchi, 1929) Gussev, 1965	*Dactylogyrus bini* Kikuchi, 1929	*Anguilla*	*japonica*	ニホンウナギ	gill	Kikuchi (1929), Katahira *et al*. (2012)	F, B
		Anguilla	*anguilla*	ヨーロッパウナギ	gill	Ogawa and Egusa (1976), Imada and Muroga (1977, 1978, 1979), Umeda *et al*. (2006)	F
		Anguilla	*marmorata*	オオウナギ	gill	Katahira and Nagasawa (2014)	F
134. *Pseudodactylogyrus haze* Ogawa, 1984		*Acanthogobius*	*flavimanus*	マハゼ	gill	Ogawa (1984b)	B
135. *Pseudodactylogyrus kamegaii* Iwashita, Hirata, and Ogawa, 2002		*Anguilla*	*japonica*	ニホンウナギ	gill	Iwasita *et al*. (2002), Katahira *et al*. (2012)	B
		Anguilla	*japonica*	ニホンウナギ	gill	Katahira *et al*. (2012)	B
Family Diplectanidae Monticelli, 1903							
136. *Lamellodiscus elegans* Bychowsky, 1957		*Acanthopagrus*	*sivicolus*	ミナミクロダイ	-	Dyer *et al*. (1989)	S
137. *Lamellodiscus japonicus* Ogawa and Egusa, 1978		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Ogawa and Egusa (1978b)	S
138. *Lamellodiscus pagrosomi* Murray, 1931		*Pagrus*	*major*	マダイ	gill	Yamaguti (1934, 1938)	S
139. *Lamellodiscus spari* Zhukov, 1970		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Ogawa and Egusa (1978b)	S
		Acanthopagrus	*sivicolus*	ミナミクロダイ	gill	Katsumata and Tamaki (1988)	S
140. *Lamellodiscus takitai* Ogawa and Eugusa, 1978		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Ogawa and Egusa (1978b)	S
141. *Lepidotrema longipenis* (Yamaguti, 1934) Kritsky, Jiménez-Ruiz and Sey, 2000	*Squamodiscns longipenis* Yamaguti, 1934	*Rhyncopelates*	*oxyrhynchus*	シマイサキ	gill	Yamaguti (1934), Ho and Perkins (1980)	S
142. *Lobotrema spari* (Yamaguti, 1958) Oliver, 1987	*Pseudomurraytrema spari* Yamagiti, 1958	*Acanthopagrus*	*schlegelii*	クロダイ	gill	Yamaguti (1958)	S
143. *Murraytrematoides ditrematis* Yamaguti, 1958		*Ditrema*	*temmincki*	ウミタナゴ	gill	Yamaguti (1958)	S
144. *Murraytrematoides lateolabracis* (Yamaguti, 1958) Oliver, 1987	*Geneticoenteron lateolabracis* Yamaguti, 1958	*Lateolabrax*	*japonicus*	スズキ	gill	Yamaguti (1958)	S
145. *Protolamellodiscus convolutus* (Yamaguti, 1953) Oliver, 1987		*Lethrinus*	*harak*	マトフエフキ	-	Dyer *et al*. (1989)	
146. *Pseudorhabdosynochus epinepheli* (Yamaguti, 1938) Kritsky and Beverley-Burton, 1986	*Diplectanum epinepheli* Yamaguti, 1938, *Pseudorhabdosynochus epinepheli* Yamaguti, 1958	*Epinephelus*	*akaara*	キジハタ	gill	Yamaguti (1938, 1958), Isshiki *et al*. (2007)	S
147. *Pseudorhabdosynochus lantauensis* (Beverley-Burton and Suriano, 1981) Kritsky and Beverley-Burton, 1986		*Epinephelus*	*akaara*	キジハタ	gill	Justine (2009)	S
148. *Pseudorhabdosynochus satyui* Justine, 2009		*Epinephelus*	*akaara*	キジハタ	gill	Justine (2009)	S
Family Tetraonchidae Bychowsky, 1937							
149. *Salmonchus alaskensis* (Price, 1937) Spassky and Roytman, 1958	*Tetraonchus alaskensis* Price, 1937	*Salvelinus*	*leucomaensis*	アメマス	gill	Ogawa (1994b)	F
150. *Salmonchus awakurai* (Ogawa and Egusa, 1978)	*Tetraonchus* (*Tetraonchus*) sp., *Tetraonchus awakurai* Ogawa and Egusa, 1978	*Oncorhynchus*	*masou masou*	ヤマメ	gill	Awakura (1966), Ogawa and Egusa (1978a, 1984), Ogawa (1994b)	F
	Tetraonchus awakurai Ogawa and Egusa, 1978	*Oncorhynchus*	*mykiss*	ニジマス	gill	Ogawa and Egusa (1978a)	F
	Tetraonchus awakurai Ogawa and Egusa, 1978	*Oncorhynchus*	*masou masou*	サクラマス	gill	Awakura *et al*. (1981)	F
	Tetraonchus awakurai Ogawa and Egusa, 1978	*Oncorhynchus*	*masou ishikawae*	アマゴ	gill	Uno (1990)	F
151. *Salmonchus oncorhynchi* (Ogawa and Egusa, 1978)	*Tetraonchus oncorhynchi* Ogawa and Egusa, 1978	*Oncorhynchus*	*masou masou*	ヤマメ	gill	Ogawa and Egusa (1978a, 1984)	F
	Tetraonchus oncorhynchi Ogawa and Egusa, 1978	*Oncorhynchus*	*masou ishikawae*	アマゴ	gill	Uno (1990)	F

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
Subclass Polyopisthocotylea Odhner, 1912							
Order Polystomatidea Lebedev, 1988							
Family Polystomatidae Gamble, 1896							
152. *Diplorchis ranae* Ozaki, 1931		*Glandirana*	*rugosa*	ツチガエル	urinary bladder	Ozaki (1931a, 1932, 1935a, b), Yamaguti (1936, 1940b), Uchida and Itagaki (1978)	F
153. *Neopolystoma exhamatum* (Ozaki, 1935) Price, 1939	*Polystomoides exhamatum* Ozaki, 1935	*Mauremys*	*japonica*	イシガメ	urinary bladder	Ozaki (1931b, 1935a)	F
		Trachemys	*scripta elegans*	ミシシッピアカミミガメ	urinary bladder	Oi *et al.* (2012)	F
154. *Polystoma integerrimum* (Floelich, 1791)	*Polystoma ozakii* Uchida, Machida, Uchida and Itagaki, 1988	*Bufo*	*japonicus formos*	アズマヒキガエル	urinary bladder	Uchida *et al* . (1988)	F
		Rana	*pirica*	エゾアカガエル	urinary bladder	Uchida and Itagaki (1980)	F
	Polystoma sp.	*Bufo*	*japonicus formos*	アズマヒキガエル	urinary bladder	Uchida and Yamamoto (1981)	F
155. *Polystoma ozakii* Price, 1939	*Polystoma integerrimum* (Floelich, 1791), *Polystoma integerrimum japonicum* Ozaki, 1940	*Rana*	*ornativentris*	ヤマアカガエル	urinary bladder	Ozaki (1935a, 1940), Goldberg and Bursey (2002)	F
	Polystoma ezoensis Uchida, Machida, Uchida and Itagaki,	*Rana*	*japonica*	ニホンアカガエル	urinary bladder	Uchida *et al* . (1988)	F
	Polystoma sp., *Polystoma ezoensis* Uchida, Machida, Uchida and Itagaki, 1988	*Rana*	*pirica*	エゾアカガエル	urinary bladder	Uchida and Itagaki (1980), Uchida *et al* . (1988), Goldberg and Bursey (2003)	F
156. *Polystoma rhacophori* Yamaguti, 1936		*Rhacophorus*	*arboreus*	モリアオガエル	urinary bladder	Yamaguti (1936)	F
		Rhacophorus	*schlegelii*	シュレーゲルアオガエル	urinary bladder	Uchida and Itagaki (1974, 1978), Uchida *et al* . (1988)	F
		Rhacophorus	*viridis viridis*	オキナワアオガエル	urinary bladder	Hasegawa (2002)	F
	Polystoma sp.	*Rhacophorus*	*viridis*	アマミアオガエル	urinary bladder	Hasegawa (1990, 2002)	F
157. *Polystomoides japonicum* Ozaki, 1935		*Mauremys*	*japonica*	イシガメ	mouth, esophagus	Ozaki (1931b, 1935a)	F
		Trachemys	*scripta elegans*	ミシシッピアカミミガメ	mouth, esophagus	Oi *et al.* (2012)	F
158. *Polystomoides megaovum* Ozaki, 1936		*Geoemyda*	*japonica*	リュウキュウヤマガメ	urinary bladder	Ozaki (1936)	F
159. *Pseudopolystoma dendriticum* (Ozaki 1948) Yamaguti, 1963	*Polystoma dendriticum* Ozaki, 1948	*Onychodactylus*	*kinneburi*	シコクハコネサンショウウオ	urinary bladder	Ozaki (1948)	F
		Onychodactylus	*japonicus*	ハコネサンショウウオ	urinary bladder	Uchida and Itagaki (1978, 1979)	F
Order Diclybothriidea Bychowsky, 1957							
Family Hexabothriidae Price, 1942							
160. *Callorhynchocotyle sagamiensis* Kitamura, Ogawa, Taniuchi and Hirose,		*Chimaera*	*phantasma*	ギンザメ	gill filaments	Kitamura *et al.* (2006)	S
161. *Erpocotyle modama* Iwata, 1991		*Triakis*	*scyllium*	ドチザメ	gill	Iwata (1990a)	S
162. *Rajonchocotyle kenojei* Yamaguti, 1938		*Raja*	*kenojei*	ガンシエイ	gill	Yamaguti (1938)	S
163. *Squalonchocotyle laymani* Yamaguti, 1958		*Mustelus*	*manazo*	ホシザメ	gill	Yamaguti (1958)	S
164. *Squalonchocotyle mitsukurii* Kitamura, Ogawa, Taniuchi and Hirose, 2006		*Squalus*	*mitsukurii*	フトツノザメ	gill filaments	Kitamura *et al.* (2006)	S
165. *Squalonchocotyle spinaci* (Goto, 1894) Cerfontaine, 1899	*Onchocotyle spinaci* Goto, 1894	*Etmopterus*	sp.	カラスザメ属の一種	gill	Goto (1894)	S
Order Mazocraeidea Bychowsky, 1937							
Family Diclidophoridae Fuhrmann, 1928							
166. *Choricotyle elongata* (Goto 1894) Llewellyn, 1941	*Diclidophora elongata* Goto, 1894	*Pagrus*	*major*	マダイ	mouth cavity	Goto (1894), Iwata (1982, 1991a)	S
	Diclidophora elongata Goto, 1894	*Cymothoa*	sp.	ウオノエ属の一種	dorsal surface	Goto (1894)	S
	Diclidophora elongata Goto, 1894	*Meinertia*	*oxyrhynchaena*	ソコウオノエ	dorsal surface	Yamaguti (1938)	S
167. *Cyclobothrium iniistii* Yarnaguti, 1937		*Xyrichtys*	*dea*	テンス	gill	Yamaguti (1937b)	S
168. *Cyclobothrium semicossyphi* Yamaguti, 1938		*Semicossyphus*	*reticulatus*	コブダイ	gill	Yamaguti (1938, 1958), Iwata (1982, 1991)	S
169. *Cyclobothrium sessile* (Goto, 1894) Cerfontaine, 1895	*Diclidophora sessile* Goto, 1894	*Semicossyphus*	*reticulatus*	コブダイ	mouth cavity, gill	Goto (1894), Yamaguti (1934)	S
170. *Diclidophora lotella* Machida, 1972	*Diclidophora* sp.	*Physiculus*	*maximowiczi*	エゾイソアイナメ	gill	Machida (1972a, b)	S
171. *Heterobothrium okamotoi* Ogawa, 1991	*Diclidophora tetrodonis* Goto, 1894	*Takifugu*	*rubripes*	トラフグ	gill	*e.g.* Okamoto (1963, 1964, 1965), Okamoto and Ogasawara (1965), Ogawa and Inoue (1997b, c), Ogawa (1991, 1997, 1998, 2000a), Wang *et al* . (1997), Tsukahara (1999), Hirazawa *et al* . (2001), Tsutsui *et al* . (2003), Nakane *et al* . (2005), Shirakashi *et al* . (2010), Kimura (2013)	S
172. *Heterobothrium tetrodonis* (Goto, 1894) Cerfontaine, 1895	*Diclidophora tetrodonis* Goto, 1895				gill	Goto (1894)	S
		Takifugu	*poecilonotus*	コモンフグ	gill	Iwata (1982, 1991)	S
		Takifugu	*paradalis*	ヒガンフグ	gill	Ogawa (1991)	S
173. *Heterobothrium yamagutii* Ogawa, 1991	*Heterobothrium tetrodonis* (Goto, 1894) Cerfontaine, 1895	*Takifugu*	*xanthopterus*	シマフグ	gill	Yamaguti (1958), Ogawa (1991)	S
174. *Neoheterobothrium hirame* Ogawa, 1999		*Paralichthys*	*olivaceus*	ヒラメ	gil, gill rake, buccal cavity wall	*e.g.* Ogawa (1999, 2000b), Yoshinaga *et al* . (2000a, b, 2001a, b, 2009), Anshary and Ogawa (2001), Anshary *et al* . (2002), Tsutsumi *et al* . (2002), Isshiki *et al* . (2003), Tomiyama *et al* . (2004), Yamamoto *et al* . (2005) Shirakasi *et al* . (2006), Yamamoto *et al* . (2011)	S
175. *Megaloncus arelisci* Yamaguti, 1958		*Cynoglossus*	*joyneri*	アカシタビラメ	gill	Yamaguti (1958)	S
176. *Osphyobothrus parapercis* Yamaguti, 1958		*Parapercis*	*pulchella*	トラギス	gill	Yamaguti (1958)	S
Family Pseudodiclidophoridae Yamaguti, 1965							
177. *Pseudodiclidophora decapteri* Yamaguti, 1965		*Decapterus*	*macarellus*	クサヤモロ	gill	Ichihara (1974)	S

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
Family Plectanocotylidae Monticelli, 1903							
178. *Octoplectanocotyla trichiuri* Yamaguti, 1937		*Trichiurus*	*japonicus*	タチウオ	gill	Yamaguti (1937b)	S
Family Mazocraeidae Price, 1936							
179. *Grubea australis* Rohde, 1987		*Scomber*	*japonicus*	マサバ	gill	Kamegai, Sh. (1990)	S
180. *Pseudokuhnia minor* (Goto, 1984) Rhode and Watson, 1985	*Octocotyle minor* Goto, 1894	*Scomber*	*japonicus*	マサバ	gill	Goto (1894)	S
181. *Kuhnia scombri* (Kuhn, 1829) Sproston, 1945	*Octocotyle major* Goto, 1894	*Scomber*	*japonicus*	マサバ	gill	Goto (1894), Ichihara *et al* . (1968), Machida *et al* . (1972)	S
182. *Kuhnia thunni* (Ishii and Sawada, 1938) Sproston, 1946	*Dactylocotyle minor* Ishii, 1936	*Thunnus*	*orientalis*	クロマグロ	gill	Ishii (1936)	S
183. *Mazocraeoides dorosomata* (Yamaguti, 1938) Sproston, 1946	*Pseudoctocotyla dorosomatis* Yamaguti, 1938	*Clupanodon*	*thrissa*	シナドロクイ	gill	Yamaguti (1938, 1942)	S
184. *Neomazocraes dorosomatis* (Yamaguti, 1938) Price, 1943	*Discocotyle dorosomatis* Yamaguti, 1938	*Clupanodon*	*thrissa*	シナドロクイ	gill	Yamaguti (1938, 1942)	S
		Konosirus	*punctatus*	コノシロ	gill	Iwata (1984)	S
Family Bychowskicotylidae Lebedev, 1969							
185. *Yamaguticotyla truncata* (Goto, 1894) Price, 1959	*Microcotyle truncata* Goto, 1894	*Parapristipoma*	*trilineatum*	イサキ	gill	Goto (1894)	S
Family Gastrocotylidae Price, 1943							
186. *Allopseudaxine katsuwonis* (Ishii, 1936) Yamaguit, 1943	*Pseudaxine katsuwonis* Ishii, 1936	*Katsuwonus*	*pelamis*	カツオ	gill	Ishii (1936)	S
187. *Allopseudaxinoides vagans* (Ishii, 1936) Yamaguit, 1968	*Pseudaxine vagans* Ishii, 1936	*Katsuwonus*	*pelamis*	カツオ	gill	Ishii (1936)	S
188. *Gastrocotyle trachuri* Van Beneden and Hesse, 1863		*Trachurus*	*japonicus*	マアジ	gill	Yamaguti (1938)	S
189. *Pseudaxine trachuri* Parona and Perugia, 1890		*Trachurus*	*japonicus*	マアジ	gill	Yamaguti (1938, 1942)	S
Family Gotocotylidae Yamaguti, 1963							
190. *Gotocotyla acanthura* (Parona and Perugia, 1896) Meserve, 1938	*Gotocotyla sawara* Ishii, 1936	*Scomberomorus*	*niphonius*	サワラ	gill	Ishii (1936)	S
Family Diplozonidae Palombi, 1949							
191. *Eudiplozoon nipponicum* (Goto, 1891) Khotenovsky, 1985	*Diplozoon nipponicum* Goto, 1891	*Carassius*	sp.	フナ属の1種	gill	*e.g.* Goto (1891), Kamegai, Sa. (1968a, b, 1970b, c, 1972, 1974a, b, 1975a, 1977a, b, 1978a, b, 1985); Ichihara *et al* . (1980, 1983); Kamegai, Sa. *et al.* (1980a, b, 1984); Kawatsu (1978), Kamegai, Sa. and Ichihara (1981b)	F
	Diplozoon nipponicum Goto, 1891	*Carassius*	*auratus*	キンギョ	gill	Kamegai, Sa. (1978b, 1985); Kamegai, Sa. and Ichihara (1981a, b); Kamegai, Sa. *et al* . (1982, 1983a, b), Timoshkin *et al* . (2011)	F
	Diplozoon nipponicum Goto, 1891	*Carassius*	*cuvieri*	ゲンゴロウブナ	gill	Kamegai, Sa. (1977a)	F
	Diplozoon nipponicum Goto, 1891	*Carassius*	*grandoculis*	ニゴロブナ	gill	Kamegai, Sa. (1975b)	F
	Diplozoon nipponicum Goto, 1891	*Carassius*	*langsdorfi*	ギンブナ	gill	Kamegai, Sa. (1975b, 1977a), Kamegai, Sa. *et al* . (1979), Mizuo *et al* . (1999), Sicard *et al* . (2003)	F
192. *Eudiplozoon nipponicum* (Goto, 1891) Khotenovsky, 1985	*Diplozoon nipponicum* Goto, 1891	*Cyprinus*	*carpio*	コイ	gill	*e.g.* Kamegai, Sa. *et al* . (1965, 1966a, b, 1967); Kamegai, Sa (1968a, b, c, 1969, 1970a, 1973, 1974a, b), Hirose *et al* . (1987), Ogawa (1994b), Timoshkin *et al* . (2011)	F
193. *Paradiplozaon skrjabini* Akhmerov, 1974	*Diplozoon* sp.	*Tribolodon*	*hakonensts*	ウグイ	gill	Kamegai, Sa. (1971, 1976), Ohkura *et al* . (1985); Ohtomo *et al* . (1985); Suzuki and Ohkura (1987, 1988), Ogawa (1994b), Shimazu *et al* . (2015)	F
	Diplozoon sp.	*Tribolodon*	*brandti*	マルタ	gill	Ogawa (1994b)	F
	Diplozoon sp.	*Tribolodon*	*sachalinensis*	エゾウグイ	gill	Ogawa (1994b), Shimazu *et al* . (2015)	F
		Rhynchocypris	*logowskii steindac*	アブラハヤ	gill	Shimazu *et al* . (2015)	F
		Rhynchocypris	*oxycephalus jouyi*	タカハヤ	gill	Shimazu *et al* . (2015)	F
Family Hexostomatidae Price, 1936							
194. *Hexostoma dissimilis* (Yamaguti, 1937) Sproston, 1946	*Hexacotyle dissimilis* Yamaguti, 1937	*Thynnus*	*orientalis*	クロマグロ	gill	Yamaguti (1937b)	S
195. *Hexostoma grossum* (Goto, 1894) Sproston, 1946	*Hexacotyle grossa* Goto, 1894	*Thunnus*	*obesus*	メバチ	gill	Goto (1894)	S
	Hexacotyle grossa Goto, 1894	*Thynnus*	*orientalis*	クロマグロ	gill	Kihara (1960)	S
196. *Homostoma acutum* (Goto, 1894) Unnithan, 1965	*Hexacotyle acuta* Goto, 1894	*Thunnus*	*obesus*	メバチ	gill	Goto (1894)	S
Family Axinidae Monticelli 1903							
197. *Axine cypseluri* (Meserve, 1938) Price 1945	*Axine* (*Axine*) *cypseluri* Yamaguti, 1940	*Cypselurus*	*agoo*	トビウオ	gill	Yamaguti (1940a)	S
198. *Axinoides aberrans* (Goto, 1894) Price, 1946	*Axine aberrans* Goto, 1894	*Ablennes*	*hians*	ハマダツ	gill	Goto (1894), Yamaguti (1934)	S
199. *Axinoides sebastisci* Yamaguti, 1958	*Axine* (*Axinoides*) *sebastisci* Yamaguti, 1958	*Sebastiscus*	*marmoratus*	カサゴ	gill	Yamaguti (1958)	S
200. *Axinoides tylosauri* Yamaguti, 1938	*Axine* (*Axinoides*) *tylosauri* Yamaguti, 1938	*Ablennes*	*hians*	ハマダツ	gill	Yamaguti (1938)	S
201. *Neoaxine constricta* (Yamaguti, 1938) Price, 1946	*Axine* (*Axine*) *constricta* Yamaguti, 1938	*Ablennes*	*hians*	ハマダツ	gill	Yamaguti (1938)	S
202. *Zeuxapta japonica* Yamaguti, 1963	*Microcotyle seriolae* Yamaguti, 1940	*Seriola*	*lalandi*	ヒラマサ	gill	Yamaguti (1940a)	S

Table. 1. Continued

Species of monogenean	Synonym reported	Host genus	Host species	Japanese name of host	Infection site	Reference	Water
Family Heteraxinidae Unnithan, 1957							
203. *Heteraxine heteroceca* (Goto, 1894) Yamaguti, 1938	*Axine heterocerca* Goto, 1894, *Axine seriola* Ishii, 1936, *Axine* sp., *Axine* (*Heteraxine*) *heterocerca* Goto, 1894	*Seriola*	*quinqueradiata*	ブリ	gill	*e.g.* Goto (1894), Yamaguti (1934, 1942), Ishii (1936), Aramaki (1962), Kobayashi (1959), Kihara (1960), Anonymous (1963, 1968), Akazaki *et al*. (1963, 1964), Kubota (1964), Akazaki (1965), Harada (1965a), Kasahara (1966, 1967a, 1971), Hoshina and Matsuato (1967a), Matsusato (1968a, b, c), Honda and Tanaka (1970), Harada and Akazaki (1971), Ogawa and Egusa (1977b, 1981a), Shirakashi *et al*. (2010)	S
204. *Heteraxinoides chinensis* (Yamaguti, 1937) Yamaguti, 1963	*Axine chinensis* Yamaguti, 1937	*Hapalogenys*	*nitens*	ヒゲソリダイ	gill	Yamaguti (1937b)	S
205. *Heteraxinoides triangularis* (Goto, 1894) Yamaguti, 1963	*Microcotyle triangularis* Goto, 1894	*Caprodon*	*schlegelii*	アカイサキ	gill	Goto (1894)	S
206. *Bicotyle reticulata* (Goto, 1894)	*Microcotyle reticulata* Goto, 1894	*Pampus*	*punctatissimus*	マナガツオ	gill	Goto (1894)	S
Family Microcotylidae Taschenberg, 1879							
207. *Aspinatrium spari* (Yamaguti, 1937) Yamaguti, 1963	*Microcotyle spauri* Yamaguti, 1937	*Acanthopagrus*	*schlegelii*	クロダイ	gill	Yamaguti (1937b, 1942), Ogawa and Egusa	S
208. *Bivagina tai* (Yamaguti, 1938) Yamaguti, 1963	*Microcotyle tai* Yamaguti, 1938	*Pagrus*	*major*	マダイ	gill	Yamaguti (1938), Fujita *et al*. (1969), Yasunaga (1981), Ogawa (1988a, b), Yasunaga (1981), Urasaki (2012)	S
	Microcotyle tai Yamaguti, 1938	*Evynnis*	*tumifrons*	チダイ	gill	Fujita *et al*. (1969)	S
209. *Diplostamenides sciaenae* (Goto, 1894) Oshmarin, 1986	*Microcotyle sciaenae* Goto, 1894	*Pennahia*	*argentata*	シログチ	gill	Goto (1894), Yamaguti (1958), Ichihara (1972)	S
210. *Microcotyle branchiostegi* Yamaguti, 1937		*Branchiostegus*	*japonicus*	アカアマダイ	gill	Yamaguti (1937a)	S
211. *Microcotyle caudata* Goto, 1894		*Sebastis*	sp.	メバル属の一種	gill	Goto (1894), Yamaguti (1934, 1938)	S
212. *Microcotyle cepolae* Yamaguti, 1937		*Cepola*	*schlegeli*	スミツキアカタチ	gill	Yamaguti (1937b)	S
213. *Microcotyle ditrematis* Yamaguti, 1940		*Ditrema*	*temmincki*	ウミタナゴ	gill	Yamaguti (1940a), Ichihara (1986)	S
	Microcotyle ditrematis Yamaguti, 1941	*Beryx*	*splendens*	キンメダイ	gill	Kihara (1960)	S
		Neoditrema	*ransonneti*	オキタナゴ	gill	Ichihara (1985)	S
		Ditrema	*viride*	アオタナゴ	gill	Ichihara (1986)	S
214. *Microcotyle elegans* Goto, 1894		*Scombrops*	*boops*	ムツ	gill	Goto (1894)	S
215. *Microcotyle fusiformis* Goto, 1894		*Enedrias*	*nebulosa*	ギンポ	gill	Goto (1894)	S
216. *Microcotyle gimpo* Yamaguti, 1958		*Enedrias*	*nebulosa*	ギンポ	gill	Yamaguti (1958)	S
217. *Microcotyle pempheri* Machida and Araki, 1977		*Pempheris*	*xanthoptera*	ミナミハタンポ	gill	Machida and Araki (1977)	S
218. *Microcotyle pomatomi* Goto, 1899	*Microcotyle pomatoi* Goto, 1894	*Etelis*	*coruscans*	ハマダイ	gill	Kihara (1960)	S
219. *Microcotyle sebastis* Goto, 1894		*Sebastes*	*vulpes*	キツネメバル	gill	Goto (1894)	S
		Sebastes	*schlegeli*	クロソイ	gill	Goto (1894)	S
		Sebastes	*schlegeli*	クロソイ	gill	Yamaguti (1934)	S
		Sebastes	*oblongus*	タケノコメバル	gill	Machida *et al*. (1972)	S
220. *Microcotyle sebastisci* Yamaguti, 1958		*Sebastiscus*	*marmoratus*	カサゴ	gill	Yamaguti (1958), Hatai *et al*. (1982), Hatai (1983)	S
		Epinephelus	*akaara*	キジハタ	gill	Yamaguti (1958)	S
		Sebastes	*ventricosus*	クロメバル	gill	Yamaguti (1958)	S
		Sebastes	*pachycephalus*	アカブチムラソイ	gill	Yamaguti (1958)	S
221. *Microcotyle tanago* Yamaguti, 1940		*Ditrema*	*temmincki*	ウミタナゴ	gill	Yamaguti (1940a)	S
222. *Polylabris acanthogobii* (Yamaguti, 1940) Mamaev and Parukhin, 1976	*Microcotyle acanthogobii* Yamaguti, 1940; *Aspinatrium acanthogobii* (Yamaguti, 1940) Yamaguti, 1963	*Acanthogobius*	*flavimanus*	マハゼ	gill	Yamaguti (1940a)	S
223. *Polylabris japonicus* Ogawa and Egusa, 1980		*Acanthopagrus*	*schlegelii*	クロダイ	gill	Ogawa and Egusa (1980b)	S
224. *Polylabris gerres* (Sandars, 1944) Mamaev and Parukhin, 1976	*Prostatomicrocotyla gerres* Machida, 1973	*Gerres*	*equulus*	クロサギ	gill	Machida (1973)	S
225. *Prosomicrocotyla chiri* (Goto, 1894) Yamaguti, 1958	*Microcotyle chiri* Goto, 1894	*Hexagrammos*	*otakii*	アイナメ	gill	Goto (1894)	S
226. *Prosomicrocotyla gotoi* (Yamaguti, 1934) Yamaguti, 1958	*Microcotyle gotoi* Yamaguti, 1934	*Hexagrammos*	*otakii*	アイナメ	gill	Yamaguti (1934, 1958)	S
227. *Solostamenides mugilis* (Vogt, 1879) Unnithan, 1971	*Microcotyle mugilis* Vogt, 1878	*Mugil*	*cephalus*	ボラ	gill	Yamaguti (1938)	S
Family Thoracocotylidae Price, 1936							
228. *Neothoracocotyle acanthocybii* (Meserve, 1938) Hargis, 1956	*Thoracocotyle coryphaenae* Yamaguti, 1938	*Coryphaena*	*hippurus*	シイラ	gill	Yamaguti (1938)	S

Table 2. List of hosts and their sampling locality.

Fish species		Locality			Number of Specimens	Data	Collecting method	Specimen state	Note
Scientific name	Japanese name	Prefecture	Water system	Latitude/longitude					
Pseudorasbora parva (Temminck and Schlegel, 1846)	モツゴ	Ibaraki	Lake Kasumigaura	36°04'05"N, 140°15'23"E	8	13 June 2014	trap net	live	
		Ibaraki	Lake Kasumigaura	36°04'05"N, 140°15'23"E	2	16 June 2014	trap net	live	
		Nara	Tomio River	34°41'50"N, 135°43'55"E	2	22 July 2012	hand net	live	
		Tottori	Kitakata River	35°21'26"N, 133°19'00"E	4	6 August 2013	hand net	live	
		Okayama	Senō River	34°36'16"N, 133°51'52"E	1	16 March 2015	angling	live	
Pseudorasbora pumila Miyadi, 1930	シナイモツゴ	Nagano	Ponds at Utabi	36°35'N, 138°06'E	10	23 July 2013	trap net	live	endemic fish
		Nagano	Ponds at Yamabuse	36°36'N, 138°05'E	1	30 July 2013	trap net	live	
Rhodeus atremius atremius (Jordan and Thompson, 1914)	カゼトゲタナゴ	Saga	Irrigation canal connected to Ushitsu River	33°16'N, 130°10'E	9	30 March 2015	hand net	live	endemic fish
		Saga	Irrigation canal connected to Ushitsu River	33°16'N, 130°10'E	4	25 May 2015	hand net	live	
Rhodeus ocellatus subsp.	バラタナゴ	Saga	Irrigation canal connected to the Ushitsu River	33°16'N, 130°10'E	7	25 May 2015	hand net	live	
Ictalurus punctatus (Rafinesque, 1818)	チャネルキャットフィッシュ	Ibaraki	Lake Kasumigaura	36°04'05"N, 140°15'23"E	1	13 June 2014	angling	fresh (killed on ice)	alien fish
Pterygoplichthys disjunctivus (Weber, 1991)	マダラロリカリア	Okinawa	Sembaru Reservoir	26°15'02.8"N, 127°45'59.3"E	3	20 September 2012	hand net, cast net	live	
		Okinawa	Sembaru Reservoir	26°15'02.8"N, 127°45'59.3"E	1	27 June 205	hand net	live	
		Okinawa	Sembaru Reservoir	26°15'02.8"N, 127°45'59.3"E	4	21 August 2015	hand net	live	
		Okinawa	the Asatomata River	26°12'24.7"N, 127°44'18.7"E	2	23 June 2015	hand net	live	
		Okinawa	Hija River	26°21'08.7"N, 127°48'28.0"E	2	26 January 2013	hand net	live	
		Okinawa	Hija River	26°21'08.7"N, 127°48'28.0"E	3	25 June 2015	hand net	live	
		Okinawa	Hija River	26°21'08.7"N, 127°48'28.0"E	5	19 August 2015	hand net	live	
Gambusia affinis (Baird and Girard, 1853)	カダヤシ	Okinawa	Irrigation canal flowing into Urauchi Bay	24°23'46"N, 123°46'17"E	10	13 October 2013	hand net	fresh (killed on ice)	Site 1, alien fish
		Saga	Irrigation canal connected to Ushitsu River	33°14'12"N, 130°11'35"E	7	20 October 2013	hand net	fresh (killed on ice)	Site 2, alien fish
		Aichi	Umeda River	34°42'55"N, 137°24'23"E	15	7 November 2013	hand net	fresh (killed on ice)	Site 3, alien fish
		Tokushima	Irrigation canals connected to Yoshino Rive	34°05'18"N, 134°35'58"E	90	6 December 2013	hand net	fresh (killed on ice)	Site 4, alien fish
		Tokushima	Irrigation canals connected to Yoshino Rive	34°06'37"N, 134°35'22"E	27	6 December 2013	hand net	fresh (killed on ice)	Site 5, alien fish
		Kyōto	Dōno River	34°55'42"N, 135°47'32"E	15	31 May 2014	hand net	fresh (killed on ice)	Site 6, alien fish

Table 3. Morphological measurements (in micrometers) of *Bivaginogyrus obscurus* (Gussev, 1955) from *Pseudorasbora pumila* and *P. parva* in Japan.

Host		*Pseudorasbora pumila*	*Pseudorasbora parva*
Number of specimens measured		16	19
		range (mean ± standard deviation)	range (mean ± standard deviation)
Body	length	128–345 (278 ± 60.0)	252–411 (319 ± 45.1)
	width	24–43 (36 ± 5.5)	36–68 (49 ± 8.1)
Pharynx	diameter	11–15 (14 ± 1.0)	12–28 (18 ± 4.2)
Copulatory organ	length	16–19 (18 ± 1.0)	16–21 (18 ± 1.3)
Accessory piece	length	10–14 (13 ± 1.1)	13–16 (14 ± 1.2)
Haptor	length	29–46 (37 ± 5.1)	28–70 (46 ± 10.0)
	width	49–136 (101 ± 25.9)	86–192 (131 ± 30.5)
Anchor	total length	23–29 (26 ± 1.7)	21–27 (23 ± 2.0)
	shaft length	20–24 (22 ± 1.2)	18–22 (19 ± 1.2)
	root length	4–8 (7 ± 1.4)	3–9 (7 ± 1.6)
	point length	9–13 (11 ± 1.1)	9–11 (10 ± 0.8)
Dorsal bar	total length	21–29 (26 ± 2.3)	22–30 (27 ± 2.4)
	total width	3–8 (5 ± 1.2)	3–6 (5 ± 1.0)
	median width	1–3 (2 ± 0.4)	1–2 (2 ± 0.2)
Ventral bar	total length	39–48 (45 ± 2.5)	37–52 (45 ± 4.2)
	total width	4–11 (6 ± 1.9)	3–10 (6 ± 1.8)
	median width	1–2 (1 ± 0.3)	1–2 (1 ± 0.3)
Hook length	Pair I	13–15 (14 ± 0.7)	13–15 (14 ± 0.7)
	Pair II	15–18 (16 ± 0.9)	14–18 (16 ± 1.0)
	Pair III	16–18 (17 ± 0.8)	15–18 (16 ± 1.0)
	Pair IV	14–17 (16 ± 0.8)	15–18 (16 ± 0.9)
	Pair V	21–25 (23 ± 1.2)	21–24 (23 ± 0.8)
	Pair VI	21–27 (24 ± 1.8)	22–25 (24 ± 0.9)
	Pair VII	16–18 (17 ± 0.7)	15–18 (16 ± 0.9)
Needle	length	6–8 (7 ± 0.7)	6–8 (7 ± 0.7)
Locality		ponds in Nagano Prefecture	Lake Kasumigaura in Ibaraki Prefecture

Table 4. Records of *Ligictaluridus pricei* as alien species in various countries.

Country	Host	Reference
Europa		
Bosnia and Herzegovina	*Ameiurus nebulous* (as *Ictalurus nebulous*)	Kiskaroly (1977)
Czech Republic	*A. nebulous* (as *I. nebulous*)	Šimková *et al.* (2003)
France	*Ameiurus melas* (as *Ictalurus melas*)	Lambert (1977)
Hungary	*A. nebulosus*	Molnar (1968)
Romania	*A. nebulosus*	Roman-Chiriac (1960)
Slovakia	*A. nebulosus*	Žitňan (1965)
Asia		
China	*Ictalurus punctatus*	Wang *et al.* (2013)
Japan	*I. punctatus*	This study
Russia	*A. nebulous* (as *I. nebulous*), *I. punctatus*	Musselius *et al.* (1976), Gussev (1985), Mirzoyeva (1988)
West Indies		
Puerto Rico	*Ameiurus catus*, *A. nebulous*, *I. punctatus*	Bunkley-Williams and Williams (1994)

Table 5. Records of *Ligictaluridus pricei* from U.S.A and Canada.

Locality	Host	Reference
U.S.A		
Alabama	*Ameiurus catus* (as *Ictalurus catus*), *A. nebulosus* (as *I. nebulosus*), *I. furcatus*, *I. punctatus*, Female *I. punctatus* × Male *I. furcatus*, *Pylodictus olivaris*, *Lepomis cyanellus*	Allison (1963), Allison and Rogers (1970), Truong (2011)
Arkansas	*Noturus exilis*	Klassen & Beverley-Burton (1985a)
California	*A. catus* (as *I. catus*), *A. natalis* (as *I. natalis*), *A. nebulosus* (as *I. nebulosus*), *A. melas* (as *I. melas*), *I. punctatus*, *Morone saxatilis*, *Chaenobryttus gulosus*	Mizelle *et al*. (1961), Miller *et al*. (1973), Hensley and Nahhas (1975)
Florida	*Ameiurus natalis* (as *Ictalurus natalis*), *A. nebulosus* (as *I. meiurus nebulosus*), *I. punctatus*,	Mueller (1936)
Gergia	*I. punctatus*	Rawson and Fox (1974)
Kansas	*A. melas* (as *I. melas*), *I. punctatus*	Cloutman (1974)
Louisiana	*A. melas*	Summers and Bennett (1938)
New York	*A. nebulosus*	Mueller (1937)
North Carolina	*A. platycephalus* (as *I. platycephalus*)	Cloutman (1978)
North Dakota	*A. melas* (as *I. melas*)	Sutherland and Holloway (1979)
Ohio	*A. nebulosus*, *A. melas*	Krueger (1954)
Oklahoma	*A. melas*, *I. punctatus*	Seamster (1938ab)
Pennsylvania	*A. nebulous* (as *I. nebulous*)	Torres and Price (1971)
Tennessee	*A. natalis*, *A. melas, I. furcatus*, *I. punctatus* (as *I. lacustris punctatus*)	Mizelle and Cronin (1943)
Texas	*A. natalis*, *I. punctatus*	Lawrence and Murphy (1967), Nowlin *et al*. (1967), Clayton and Schlueter (1970), Meade and Bedinger
Virginia	*A. nebulous* (as *A. n. nebulosus*)	Hargis (1952, 1953)
Wisconsin	*I. punctatus* (as *Ictalurus l. lacustris*)	Mizelle and Regensberger (1945), Mizelle and Klucka (1953), Mizelle and Webb (1953)
Lake Erine	*I. punctatus*	Baker and Crites (1976)
Canada		
Manitoba	*A. nebulous* (as *I. nebulous*)	Lubinsky and Loch (1979)
New Brunswick	*A. nebulous* (as *I. nebulous*)	Cone (1980)
Ontario	*A. nebulosus* (as *I. nebulosus*), *N. gyrinus*	Dechtiar (1972b), Hanek and Fernando (1972), Molnar *et al*. (1974), Klassen & Beverley-Burton
Great Lakes	*A. nebulosus* (as *I. nebulosus*), *I. punctatus*, *N. gyrinus*, *N.*	Nepszy (1988)

Table 6. Prevalence and intensity deviation, range) of *Salsuginus seculus* from *Gambusia affinis* at six sites in Japan.

Site	Prefecture	Latitude/longitude	Salinity (%)	Number of fish examined	Prevarence (%)	Intensity (range)
1	Okinawa	24°23'46"N, 123°46'17"E	-	10	33.3	1.0 ± 0.0 (1)
2	Saga	33°14'12"N, 130°11'35"E	-	7	42.9	5.0 ± 3.6 (2–9)
3	Aichi	34°42'55"N, 137°24'23"E	-	15	46.7	2.4 ± 2.1 (1–6)
4	Tokushima	34°06'37"N, 134°35'22"E	0.3	90	4.4	1.0 ± 0.0 (1)
5	Tokushima	34°05'18"N, 134°35'58"E	0.7	27	0.0	-
6	Kyōto	34°55'42"N, 135°47'32"E	-	15	20.0	1.0 ± 0.0 (1)

Table 7. List of monogeneans parasitic on introduced freshwater fishes in Japan

Host	Monogenean parasite	Locality (Prefecture)	Origin	Reference
Siluriformes				
Ictalurus punctatus (Rafinesque, 1818)	*Ligictaluridus pricei* (Mueller, 1936)	Ibaraki	North America	Nittta and Nagasawa (2015b)
Loricariidae				
Pterygoplichthys disjunctivus (Weber, 1991)	*Heteropriapulus heterotylus* (Jogunoori, Kritsky and Venkatanarasaiah, 2004)	Okinawa	South America ?	Nitta and Nagasawa (2013, 2016c)
	Unilatus unilatus Mizelle and Kritsky, 1967	Okinawa	South America ?	Nitta and Nagasawa (2016c)
	Unilatus brittani Mizelle, Kritsky, and Crane, 1968	Okinawa	South America ?	Nitta and Nagasawa (2016c)
	Trinigyrus peregrinus Nitta and Nagasawa, 2016	Okinawa	South America ?	Nitta and Nagasawa (2016c)
Cyprinodontiformes				
Poeciliidae				
Gambusia affinis (Baird and Girard, 1853)	*Salsuginus seculus* (Mizelle and Arcadi, 1945)	Okinawa, Saga, Tokushima, Kyōto,	U.S.A.	Nitta and Nagasawa (2014c)
Perciformes				
Centrarchidae				
Lepomis macrochirus Rafinesque, 1819	*Actinocleidus fergusoni* Mizelle, 1938	Hiroshima	U.S.A.	Maneepitaksanti and Nagasawa (2012a)
	Onchocleidus ferox (Mueller, 1934)	Hiroshima, Shiga	U.S.A.	Muroga *et al* . (1980), Grygier and Urabe (2003)
	Onchocleidus disper Mueller, 1936	Hiroshima	U.S.A.	Maneepitaksanti and Nagasawa (2013)
Micropterus salmoides Lacépède, 1802	*Onchocleidus furcatus* (Mueller, 1937)	Shiga	U.S.A.	Grygier and Urabe (2003)
	Onchocleidus helicus Mueller, 1936	Shiga	U.S.A.	Grygier and Urabe (2003)
	Syncleithrium fusiformis (Mueller, 1934)	Shiga	U.S.A.	Grygier and Urabe (2003)
Cichlidae				
Oreochromis mossambicus (Peters, 1852)	*Cichlidogyrus halli* (Price and Kirk, 1967)	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)
	Cichlidogyrus sclerosus Paperna and Thurston,	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)
	Cichlidogyrus tilapiae Paperna, 1960	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)
O . *niloticus* (Linnaeus, 1758)	*C* . *sclerosus*	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)
	C . *halli*	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)
	C . *tilapiae*	Okinawa	Africa	Maneepitaksanti and Nagasawa (2012b)

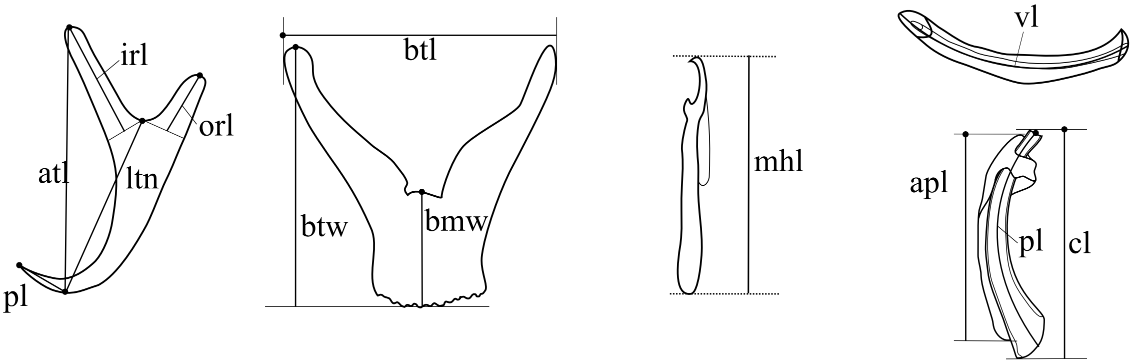

Fig. 1. Measurement axes of hard parts of *Dactylogyrus* and *Ancyrocephalus*. Abbreviations: apl, accessory piece length; atl, anchor total length; bmw, bar median width; btl, bar total length; btw, bar total width; cl, copulatory organ length; hl, marginal hook length; irl, inner root length; ltn, length to notch; orl, outer root length; pl, point length; ptl, penis tube length.

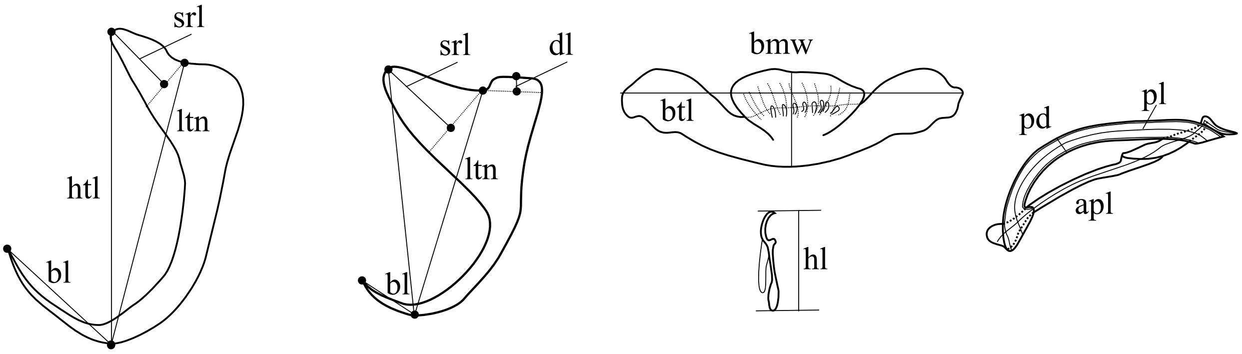

Fig. 2. Measurement axes of hard parts of *Ligictaluridus* and *Salsuginus*. Abbreviations: apl, accessory piece length; bl, blade length; bmw, bar median width; btl, bar length; dl, deep root length; htl, hamulus total length; ltn, length to notch; mhl, marginal hook length; pd, penis diameter; pl, penis length; srl, superficial root length.

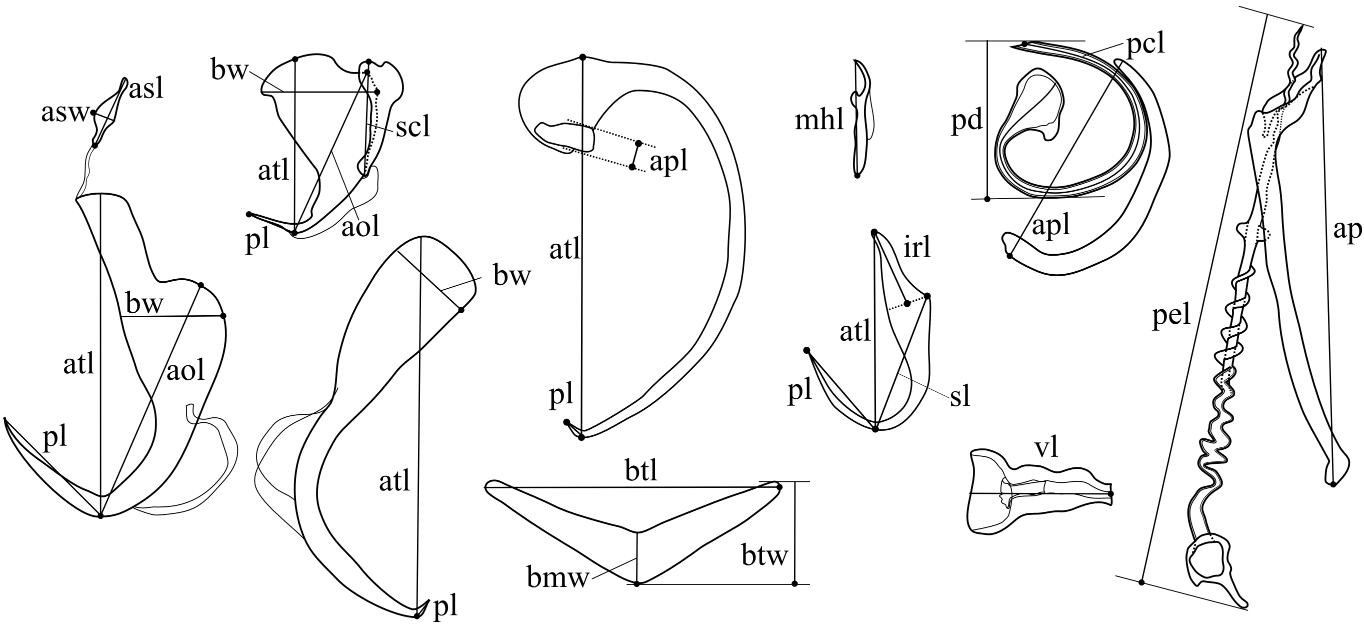

Fig. 3. Measurement axes of hard parts of *Unilatus*, *Trinigyrus* and *Heteropriapulus*. Abbreviations: aol, anchor outer length; apl, accessory piece length; asl, accessory structure length; asw, accessory structure width; atl, anchor total length; bmw, bar median width; btl, bar total length; btw, bar total width; bw, base width; copulatory organ diameter; mhl, marginal hook length; pcl, penis curve length; cd, pl, point length; pel, penis length; scl, sclerotized cup length; vl, vagina length.

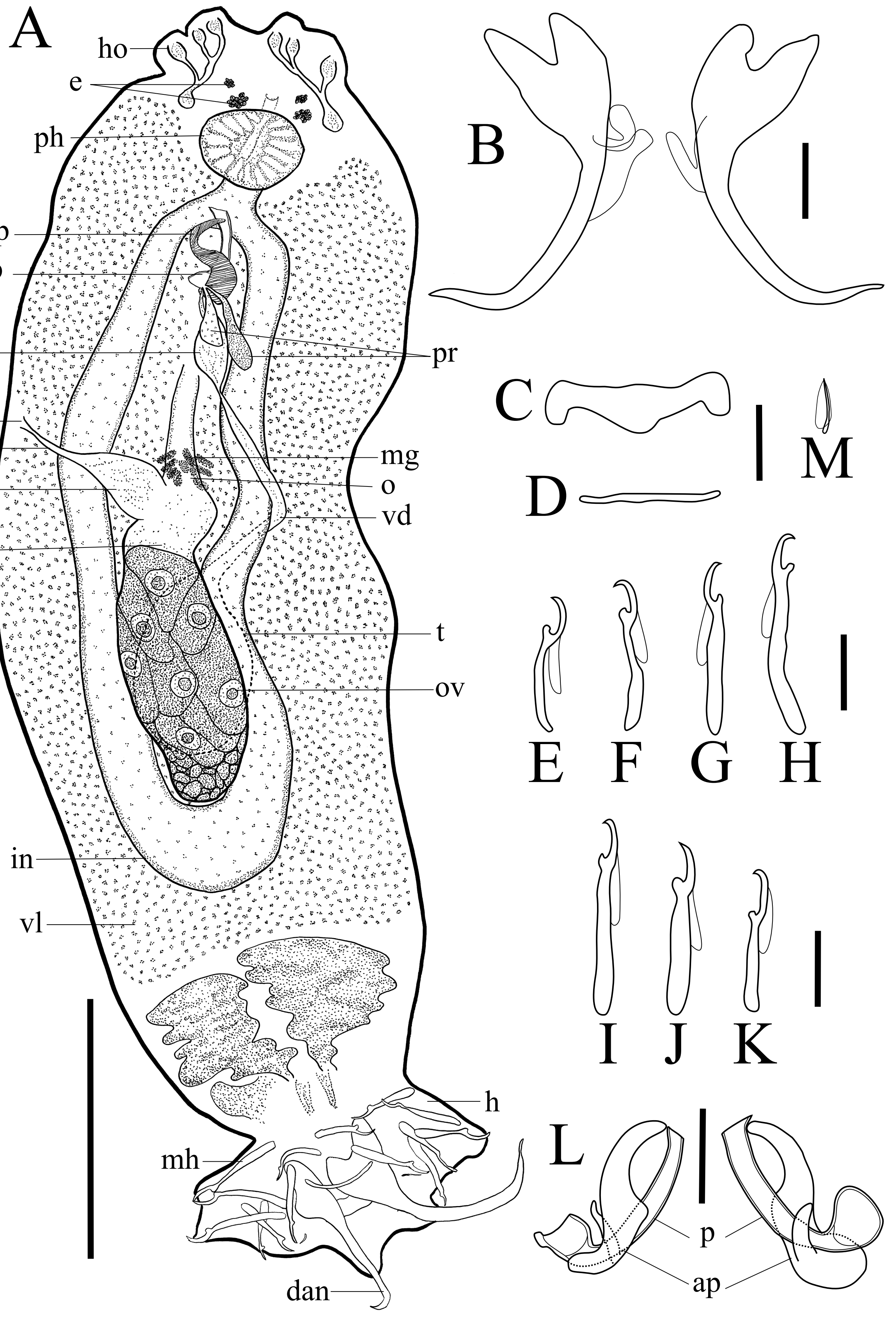

Fig. 4. *Dactylogyrus squameus* Gussev, 1955, NSMT-Pl 6179 for A, NSMT-Pl 6176 for B–M. A, whole mount (ventral view); B, dorsal anchors; C, dorsal bar; D, ventral bar; E, marginal hook of pair I; F, marginal hook of pair II; G, marginal hook of pair III; H, marginal hook of pair IV; I, marginal hook of pair V; J, marginal hook of pair VI; K, marginal hook of pair VII; L, male copulatory organs (from two specimens, left: ventral view, right: dorsal view); M, needle. Scale bars: A, 50 µm; B–M, 10 µm. Abbreviations: ap, accessory piece; dan, dorsal anchor; e, eye-spots; h, haptor; ho, head organ; in, intestine; mg, Mehlis' gland; mh, marginal hook; o; oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sr, seminal reservoir; sv, seminal vesicle; t, testis; va, vagina; vd, vas deferens; vl, vitellaria; vo, vaginal opening.

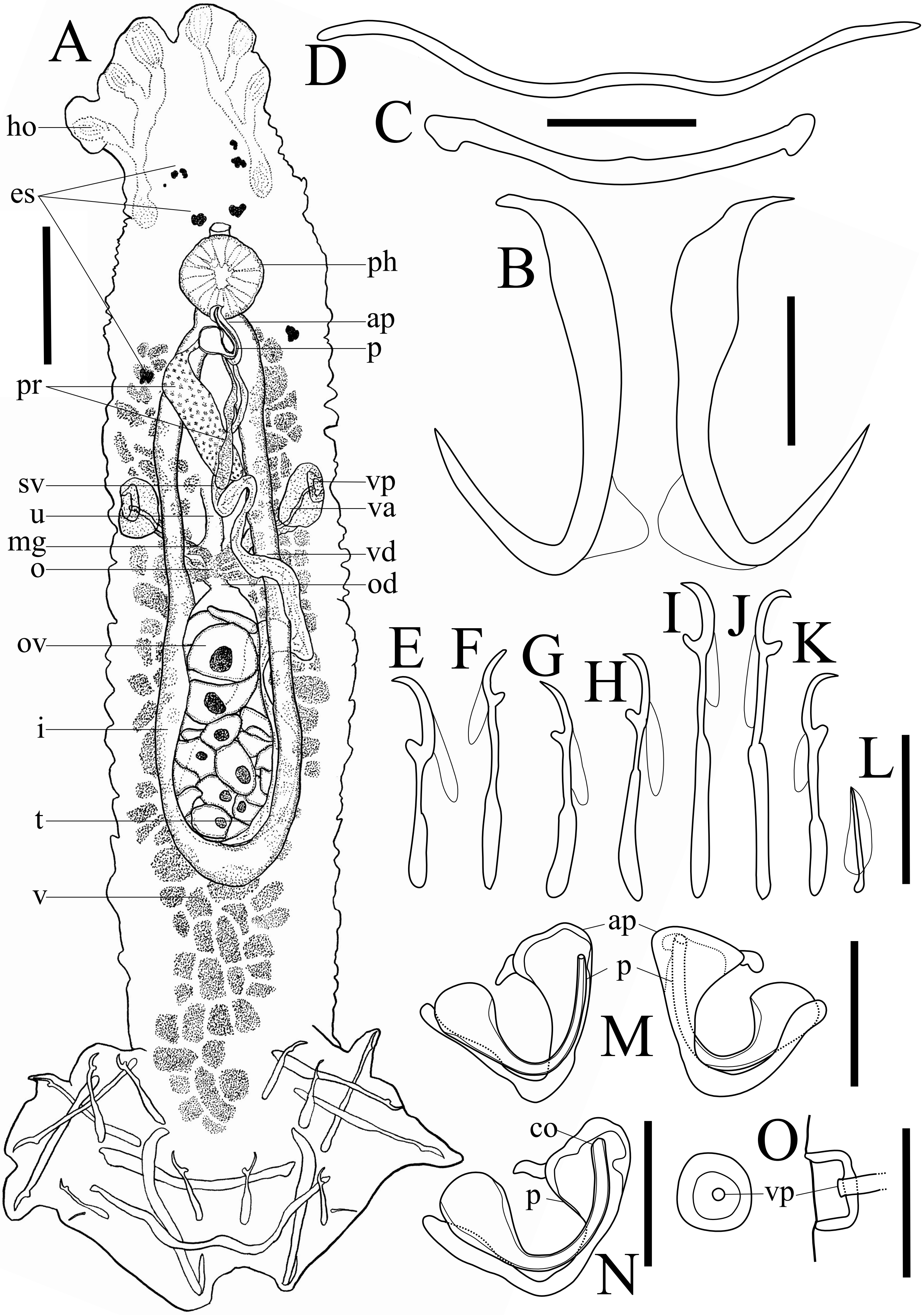

Fig. 5. *Bivaginogyrus obscurus* (Gussev, 1955). NMST-Pl 6132 for A and NMST-Pl 6131 for B–M and O (from *Pseudorasbora pumila* Miyadi, 1930); NMST-Pl 6134 for N [from *Pseudorasbora parva* (Temminck and Schlegel, 1846)]. A, whole mount (ventral view); B, anchors; C, dorsal bar; D, ventral bar; E, hook of pair I; F, hook of pair II; G, hook of pair III; H, hook of pair IV; I, hook of pair V; J, hook of pair VI; K, hook of pair VII; L, needle; M, copulatory organs of *B. obscurus* from *P. pumila* (from two specimens); N, copulatory organ of *B. obscurus* from *P. parva*; O, vaginal pore (left, front view; right, lateral view). Scale bars: A, 20 µm; B–O, 10 µm. Abbreviations: ap, accessory piece; es, eye-spot; ho, head organ; i, intestine; mg, Mehlis' gland; o; oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sv, seminal vesicle; t, testis; u, uterus; v, vitellaria; va, vagina; vp, vaginal pore; vd, vas deferens.

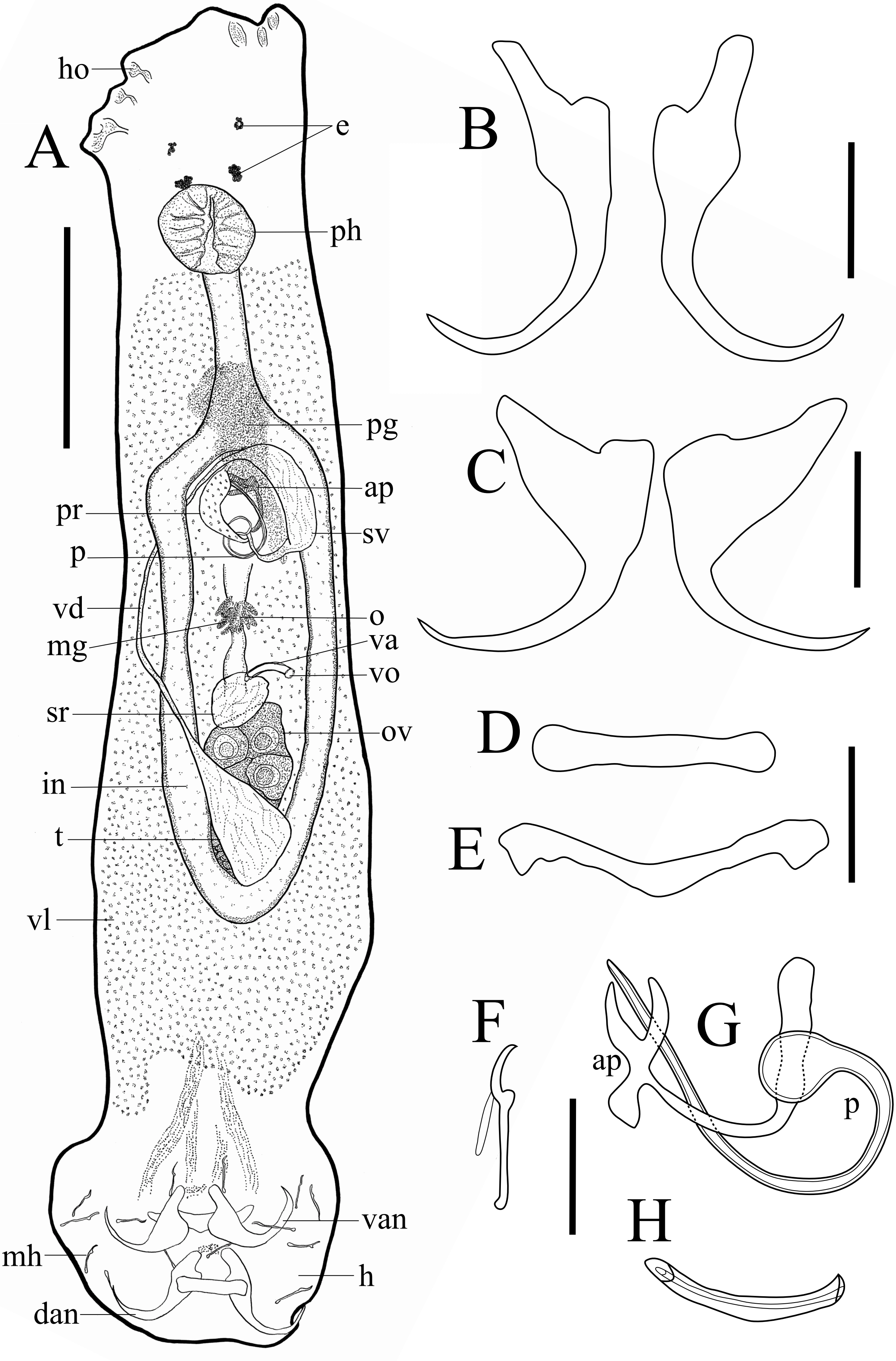

Fig. 6. *Ancyrocephalus pseudorasborae* Achmerow, 1952, NSMT-Pl 6180. A, whole mount (dorsal view); B, dorsal anchors; C, ventral anchors; D, dorsal bar; C, ventral bar; F, marginal hook; G, male copulatory organ; H, vagina. Scale bars: A, 50 µm; B–H, 10 µm. Abbreviations: ap, accessory piece; dan, dorsal anchor; e, eye-spots; h, haptor; ho, head organ; in, intestine; mg, Mehlis' gland; mh, marginal hook; o, oötype; ov, ovary; p, penis; pg, prostatic gland; ph, pharynx; pr, prostatic reservoir; sr, seminal reservoir; sv, seminal vesicle; t, testis; va, vagina; van, ventral anchor; vd, vas deferens; vl, vitellaria; vo, vaginal opening.

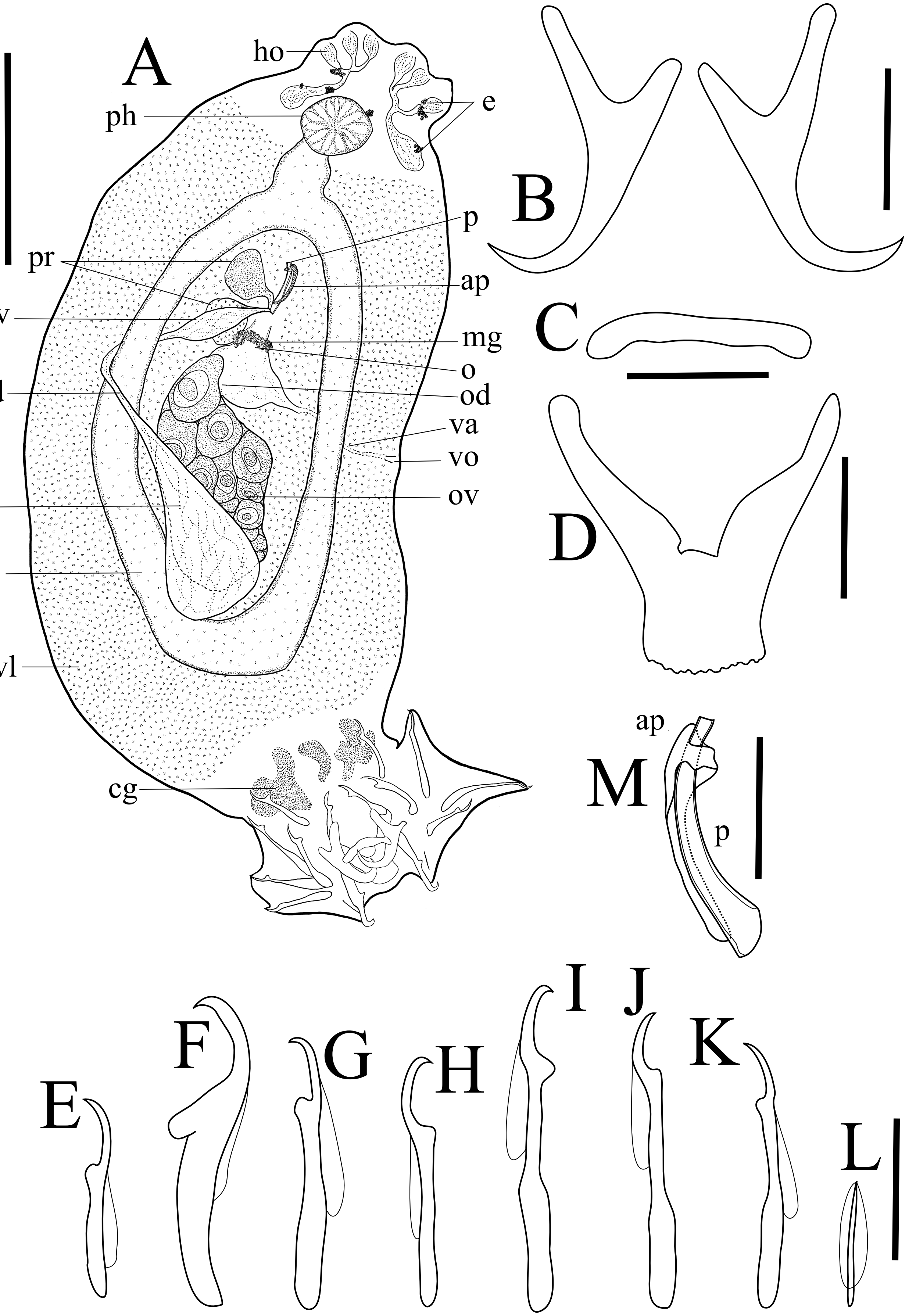

Fig. 7. *Dactylogyrus bicorniculus* Nitta and Nagasawa, 2016. Holotype NMST-Pl 6185 for B–M and paratype, NMST-Pl 6186 for A. A, whole mount (dorsal view); B, dorsal anchors; C, dorsal bar; D, ventral bar; E, marginal hook of pair I; F, hook of pair II; G, hook of pair III; H, hook of pair IV; I, hook of pair V; J, hook of pair VI; K, hook of pair VII; L, needle; M, copulatory organ. Scale bars: A, 50 µm; B–M, 10 µm. Abbreviations: ap, accessory piece; cg, cement gland; e, eye-spots; ho, head organ; in, intestine; mg, Mehlis' gland; o, oötype; ov, ovary; p, penis; pg, prostatic gland; ph, pharynx; sr, seminal reservoir; sv, seminal vesicle; t, testis; va, vagina; vd, vas deferens; vl, vitellaria; vo, vaginal opening.

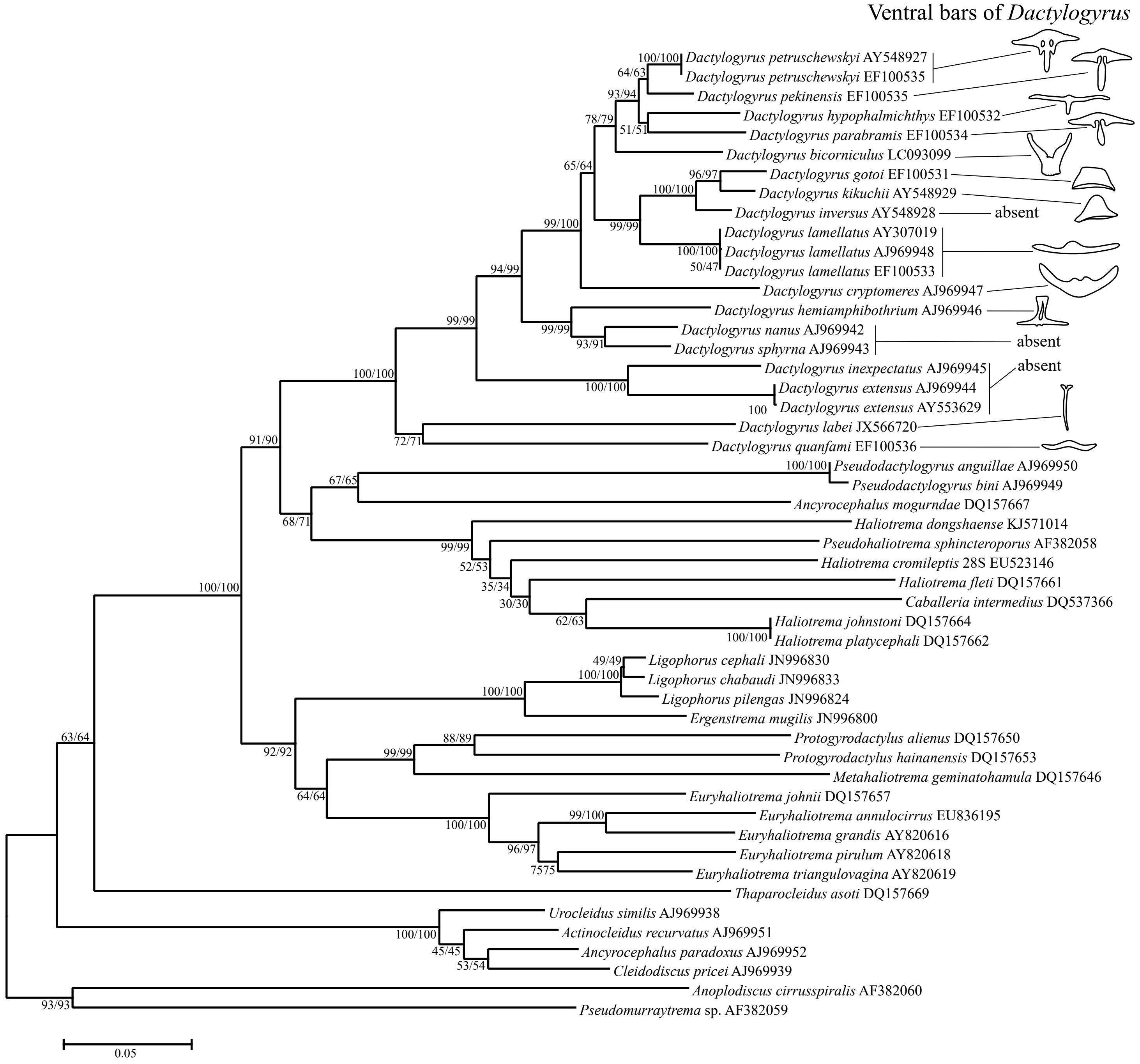

Fig. 8. Phylogenetic tree based on 28S rDNA partial sequences. The tree was constructed using neighbor-joining method. The numbers along the branches indicate bootstrap values obtained from NJ and ME methods in 1000 bootstrap replications. Drawings of ventral bars were cited from Galli *et al*. (2010), Wu *et al*. (2000), Chiary *et al*. (2014) and Nitta and Nagasawa (2014a).

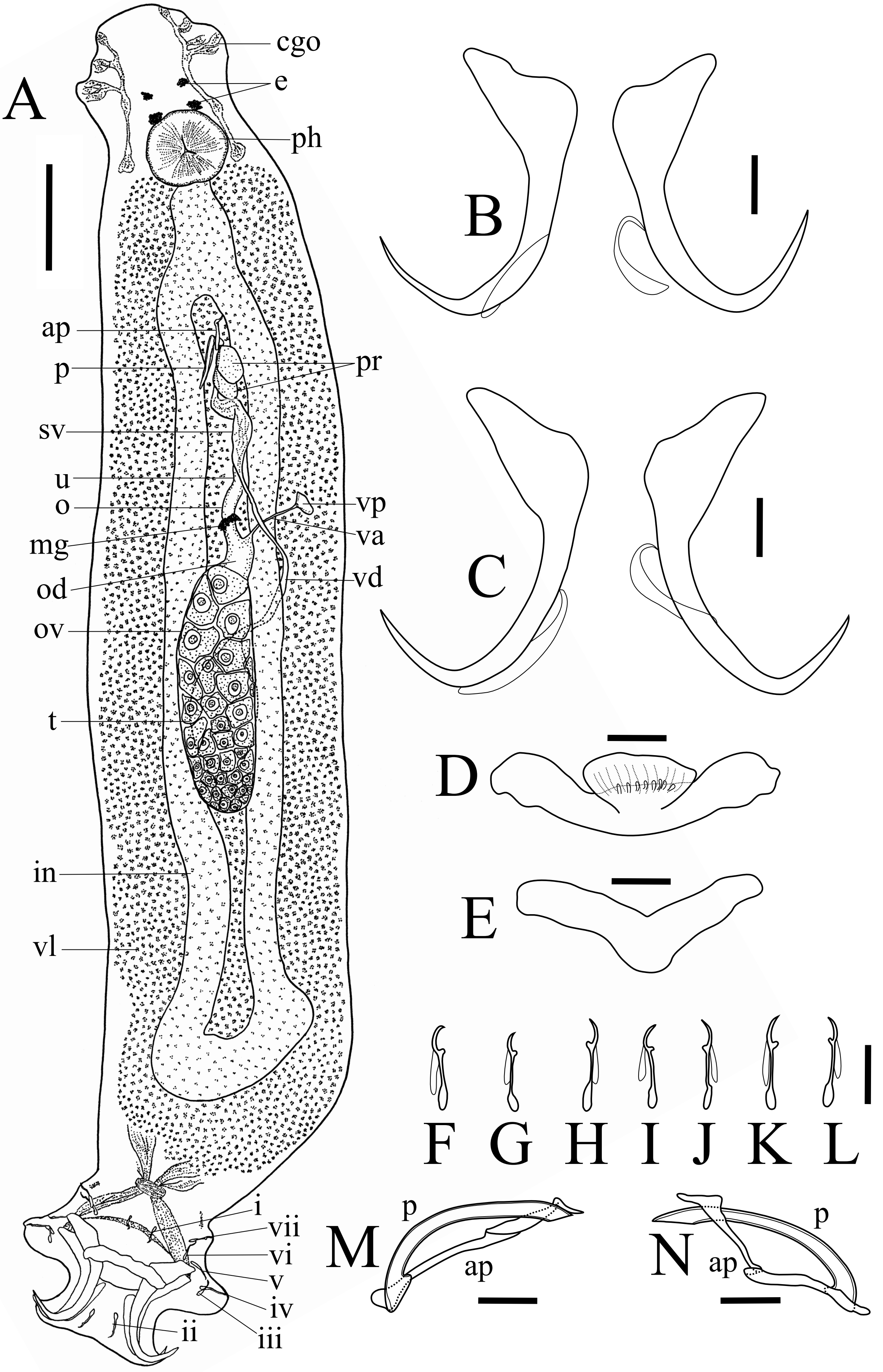

Fig. 9. *Ligictaluridus pricei* (Mueller, 1936). NSMT-Pl 6166. A, Whole mount (ventral view); B, dorsal hamuli; C, ventral hamuli; D, dorsal bar; E, ventral bar; F, marginal hook of pair I; G, marginal hook of pair II; H, marginal hook of pair III; I, marginal hook of pair IV; J, marginal hook of pair V; K, marginal hook of pair VI; L, marginal hook of pair VII; M and N, penes and accessory pieces from two specimens. Scale bars: A, 50 µm; B–N, 10 µm. Abbreviations: ap, accessory piece; cgo, opening of cephalic gland; e, eye; i, marginal hook of pair I; ii, marginal hook of pair II; iii, marginal hook of pair III; in, intestinal caeca; iv, marginal hook of pair IV; mg, Mehlis' gland; o, oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sv, seminal vesicle; t, testis; u, uterus; v, marginal hook of pair V; vi, marginal hook of pair VI; vii, marginal hook of pair VII; vl, vitellaria; va, vagina; vp, vaginal pore; vd, vas deferens.

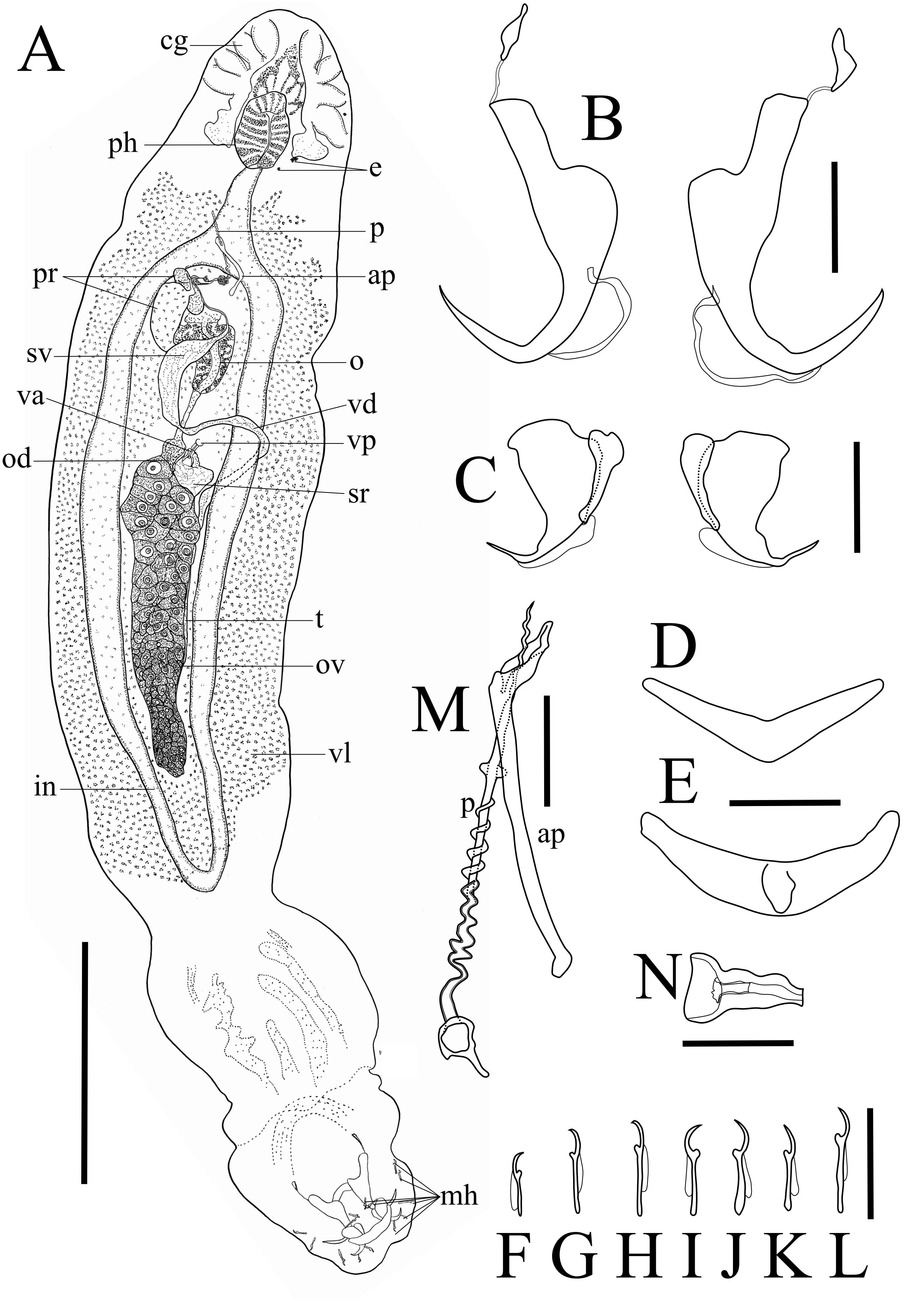

Fig. 10. *Unilatus unilatus* Mizelle and Kritsky, 1967. NSMT-Pl 6188 and 6189 for A and B–N, respectively. A, whole mount (ventral view); B, anterior anchors; C, posterior anchors; D, anterior bar; E, posterior bar; F, marginal hook of pair I; G, marginal hook of pair II; H, marginal hook of pair III; I, marginal hook of pair IV; J, marginal hook of pair V; K, marginal hook of pair VI; L, marginal hook of pair VII; M, male copulatory organ; N, vagina. Scale bars: A, 200 µm; B–N, 20 µm. Abbreviations: ap, accessory piece; cg, cephalic glands; e, eye; in, intestinal caecum; mh, marginal hook; o, oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sr, seminal reservoir; sv, seminal vesicle; t, testis va, vagina; vd, vas deferens; vl, vitellaria; vp, vaginal pore.

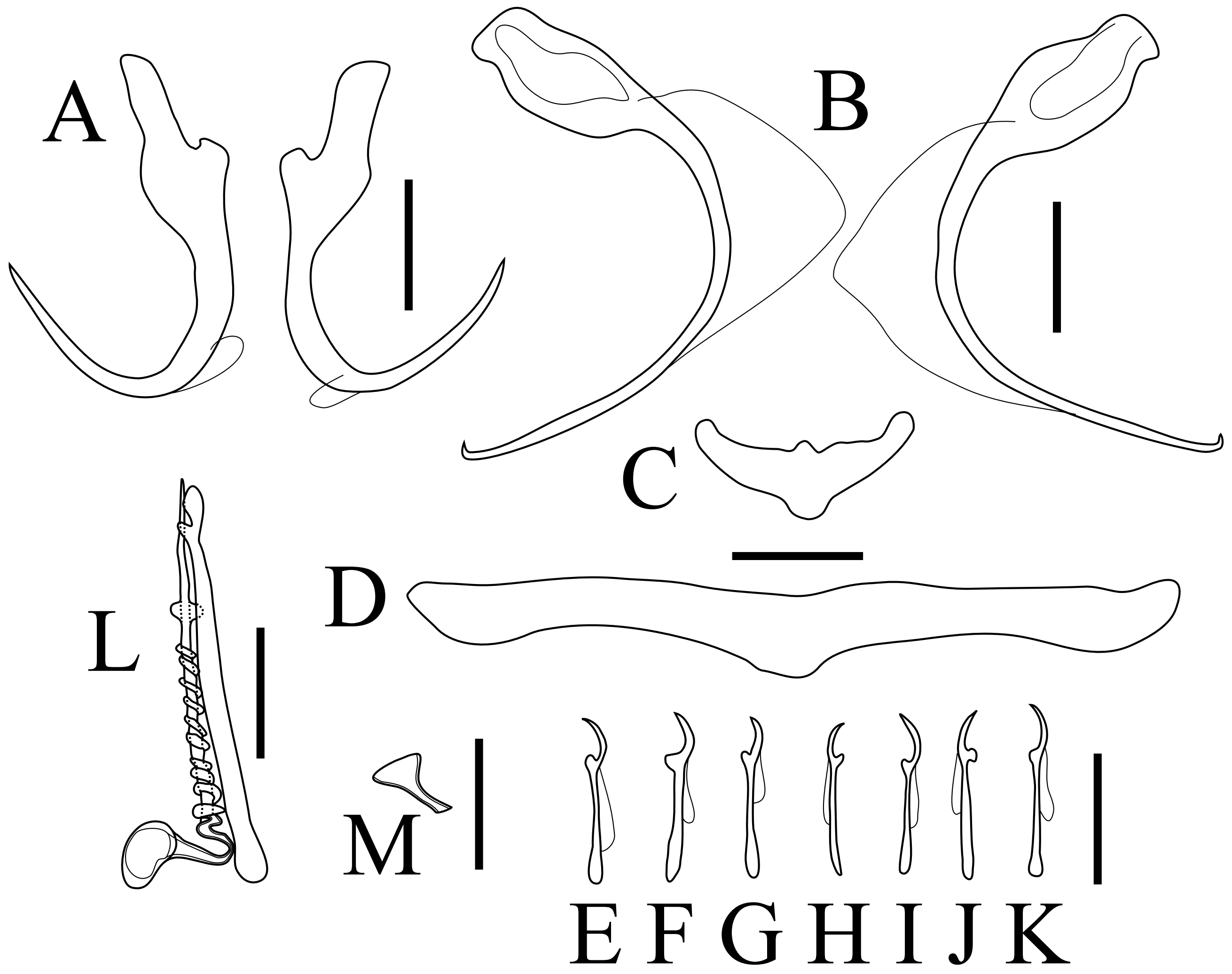

Fig. 11. *Unilatus brittani* Mizelle, Kritsky, and Crane, 1968. NSMT-Pl 6193. A, anterior anchors; B, posterior anchors; C, anterior bar; D, posterior bar; E, marginal hook of pair I; F, marginal hook of pair II; G, marginal hook of pair III; H, marginal hook of pair IV; I, marginal hook of pair V; J, marginal hook of pair VI; K, marginal hook of pair VII; L, male copulatory organ; M, vagina. Scale bars: 10 μm.

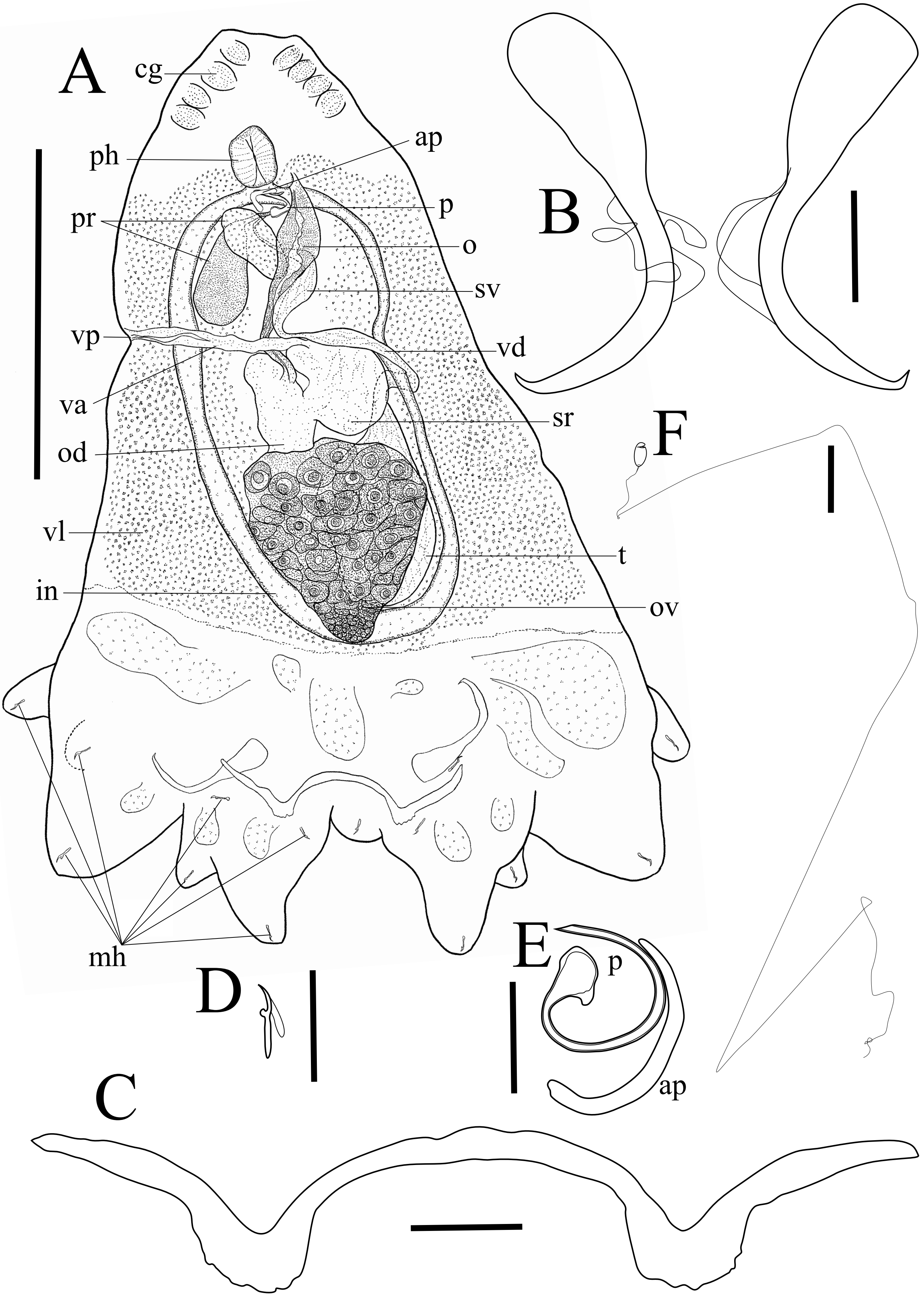

Fig. 12. *Trinigyrus peregrinus* Nitta and Nagasawa, 2016. Holotype (NSMT-Pl 6195) for B–E, paratypes for A (NSMT-Pl 6198, 6200) and for F (NMST-Pl 6202). A, whole mount (ventral view, composite); B, anchors; C, bar; D, marginal hook; E, male copulatory organ; F, egg. Scale bars: A and F, 200 µm; B–E, 20 µm. Abbreviations: ap, accessory piece; cg, cephalic glands; in, intestinal caecum; mh, marginal hook; o, oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sr, seminal reservoir; sv, seminal vesicle; t, testis; va, vagina; vd, vas deferens; vl, vitellaria; vp, vaginal pore.

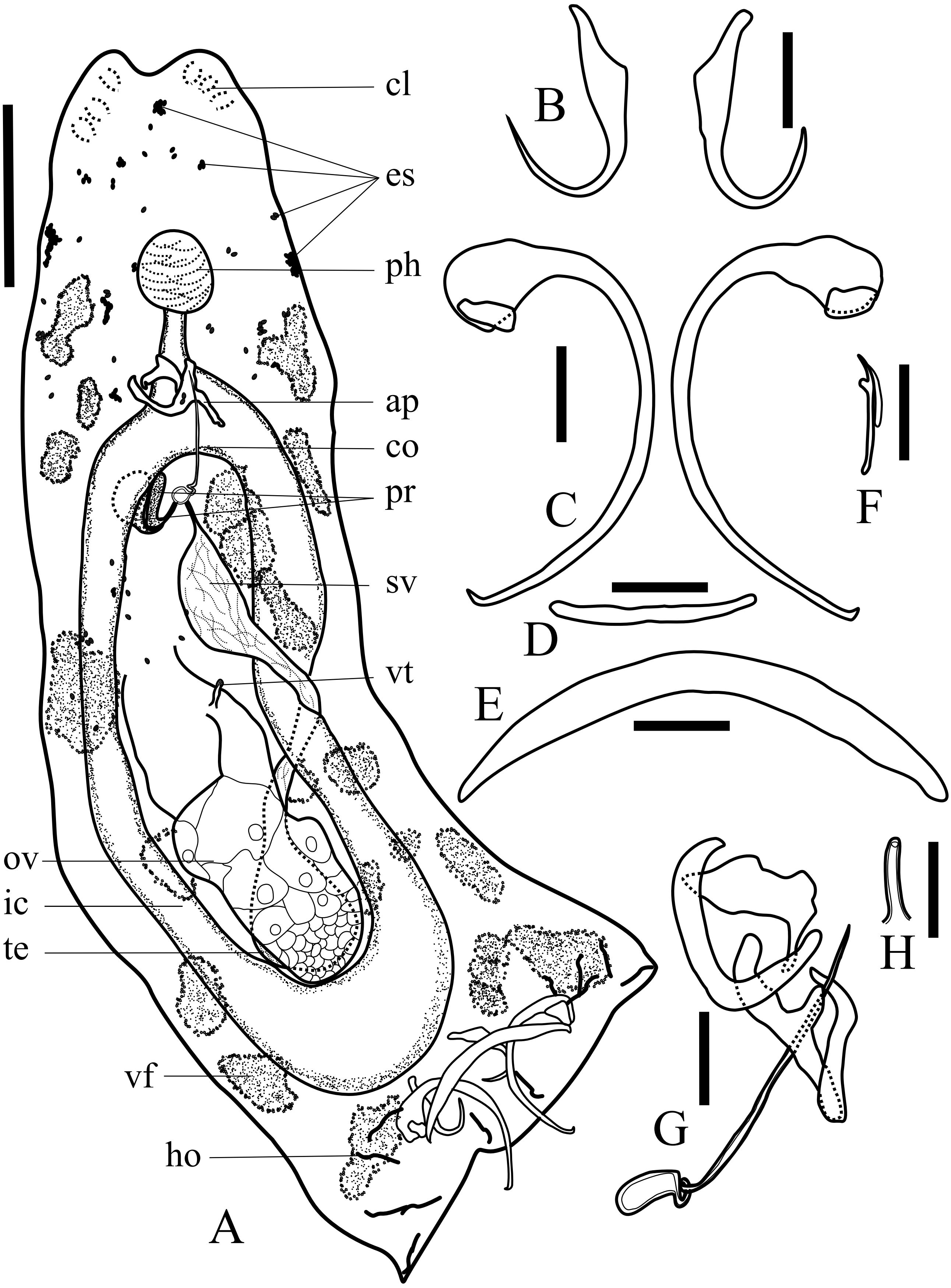

Fig. 13. *Heteropriapulus heterotylus* (Jogunoori, Kritsky, and Venkatanarasaiah, 2004). A, Whole mount (ventral view); B, dorsal anchors; C, ventral anchors; D, dorsal bar; E, ventral bar; F, hook; G, male copulatory organ; H, vagina. Scale bars: A, 50 µm; B–G, 10 µm. Abbreviations: ap, accessory piece; cl, cephalic lob; co, copulatory organ; es, eye-spot (black, ventral; gray, dorsal); ho, hook; ic, intestinal caeca; ov, ovary; ph, pharynx; pr, prostatic reservoir; sv, seminal vesicle; te, testis; vf, vitelline follicles; vt, vagina.

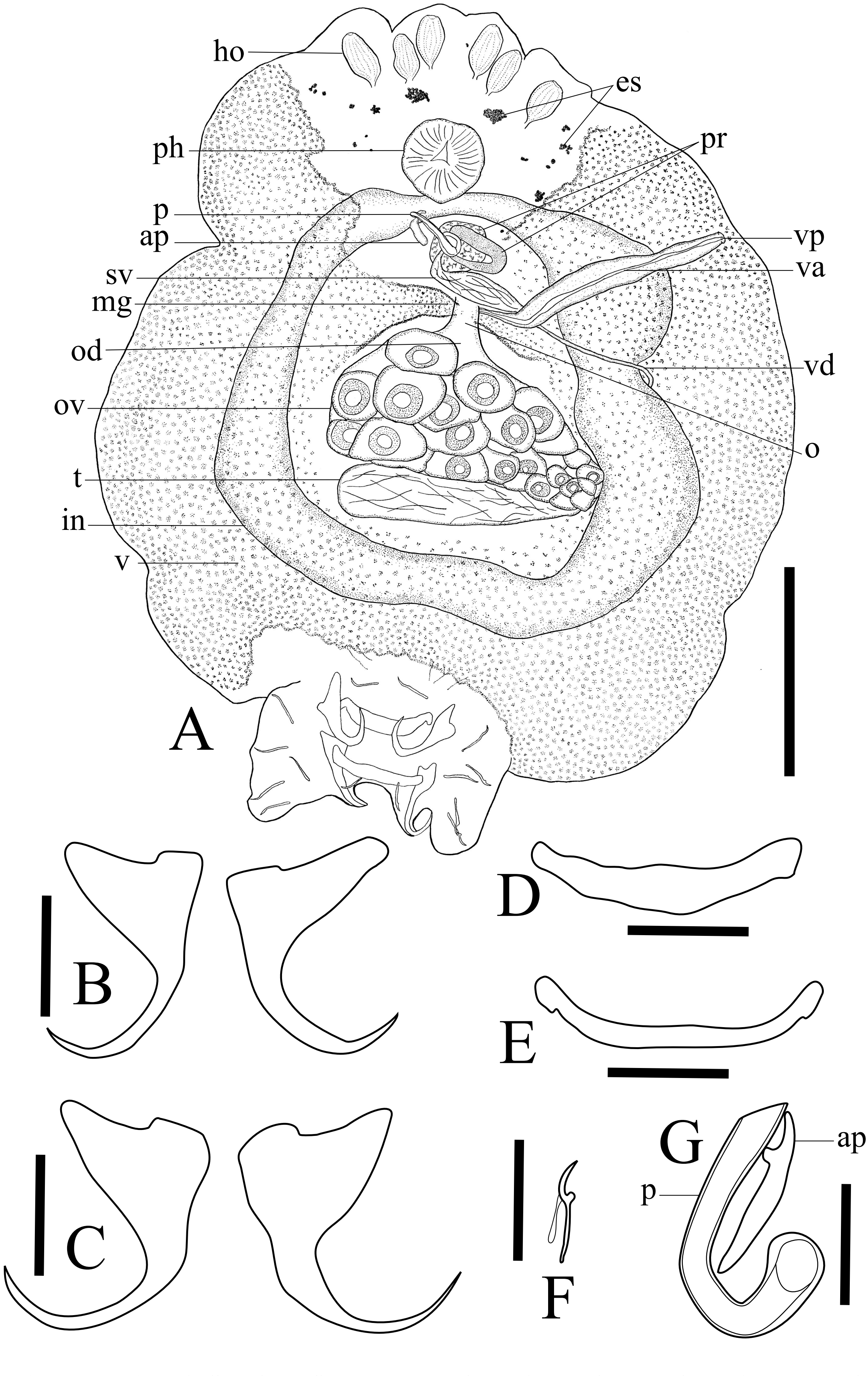

Fig. 14. *Salsuginus seculus* (Mizelle and Arcadi, 1945). NMST-Pl 6129 for A and NMST-Pl 6141 for B–G. A, whole mount (ventral view); B, dorsal hamulus; C, ventral hamulus; D, dorsal bar; E, ventral bar; F, larval hook; G, male copulatory organ; Scale bars: A, 50 µm; B–G, 10 µm. Abbreviations: ap, accessory piece; es, eye-spot; ho, head organ; in, intestinal caeca; mg, Mehlis' gland; o, oötype; od, oviduct; ov, ovary; p, penis; ph, pharynx; pr, prostatic reservoir; sv, seminal vesicle; t, testis; v, vitellaria; va, vagina; vp, vaginal pore; vd, vas deferens.