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A New Species of *Lagochondria* (Crustacea: Copepoda) Parasitic on Callionymid Fish: First Record of Precopulatory Mate Guarding in Fish-parasitic Cyclopoid Copepods, and of the Occurrence of the Genus in the North Pacific

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A new species of the genus *Lagochondria* of the parasitic cyclopoid family Chondracanthidae is described from the gill cavity of the callionymid *Repomucenus virgis* (Jordan and Fowler, 1903) collected from off Kii Peninsula, Japan. This is the first record of the occurrence of the genus from the North Pacific, and is only the second species in the genus. The female of the new species is easily distinguished from that of the Australian type species *L. nana* Ho and Dojiri, 1988 by having a squared trunk lacking paired posterior processes, and by the very short neck. In the male, the new species can be differentiated from the type species by having three inner setae on the caudal ramus, and by the distal segment of the antennule having a setal formula of 4, 3, 7+ae. An adult female was accompanied by an attached adult male, whereas fourth and fifth copepodid females each carried a fifth and a fourth attached copepodid male, respectively. This is the first record of precopulatory mate guarding in a cyclopoid family parasitic on fish hosts, and of mate guarding between late copepodids of both sexes. The zoogeography of the genus and its relatives with an atrophied tip on the antenna is also discussed.

Key words: Callionymidae, Chondracanthidae, Copepoda, *Lagochondria*, precopulatory mate guarding, zoogeography

INTRODUCTION

The Chondracanthidae Milne Edwards, 1840 is one of the largest families of parasitic copepods, and currently accommodates 51 genera and ca. 136 species (Walter and Boxshall, 2018). Within this family, two subfamilies Chondracanthinae and Lernentominae, were recognized by Oakley in Leigh-Sharpe and Oakley (1927). Ho (1970) carefully redefined these two subfamilies, and revised the attribution of genera in these taxa. However, according to Østergaard et al.'s (2003) phylogenetic analysis, Lernentominae was synonymized to Chondracanthinae. In addition, the family Pharodidae Illg, 1948, which was originally established as a subfamily of the Chondracanthidae and subsequently raised to familial rank by Ho (1971), was relegated to a junior synonym of the Chondracanthidae based on the same analysis (Østergaard et al., 2003). According to Nagasawa et al. (2013), 20 genera and 48 described species have been

recorded from fishes collected from Japanese waters.

Female chondracanthids are highly transformed, and the dwarf males are usually found attached to the genital areas of their respective females (Østergaard, 2003; Østergaard and Boxshall, 2004). Females of the family mainly parasitize the oral and gill cavities of demersal fish, and only rarely the nasal cavities and body surface (Ho, 1970; Østergaard, 2003; Boxshall and Halsey, 2004; Nagasawa et al., 2013).

During a research cruise of TRV Seisui-maru (Mie University) off Kii Peninsula, Japan, one individual of the callionymid *Repomucenus virgis* (Jordan and Fowler, 1903) was collected with a dredge, and its gill cavity was infested by an undescribed chondracanthid copepod. Only two species of chondracanthids have hitherto been recorded from callionymids from Japan: *Acanthocondria fissicauda* Shiino, 1955 from *Repomucenus curvicornus* Valenciennes, 1837 and *Acanthocondria* sp. from *R. valenciennesi* (Temminck and Schlegel, 1845) by Nagasawa et al. (2013). The latter was identified as identical to *A. fissicauda* by Nagasawa et al. (2013).

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The chondracanthid genus *Lagochondria* was first described from a specimen collected from a callionymids, *Callionymus* sp. (certainly misidentified, as the genus is restricted to the northeastern Atlantic based on Nakabo [1982]), captured from the Arafura Sea, Australia (Ho and Dojiri, 1988). The present specimens can be classified as an undescribed species of the genus *Lagochondria* on the basis of the body tagmosis and the morphology of the antenna and legs of both sexes. This is the first record of the occurrence of the genus in Japanese waters, and constitutes only the second species in the genus. Both sexes of the new species are described herein. A unique reproductive behavior and the zoogeography of the genus are also discussed.

MATERIALS AND METHODS

The demersal host fish *Repomucenus virgis* was collected with a dredge (mouth area 30 cm [height] × 100 cm [width]; 4 mm-mesh) at a depth of 82 m off the eastern side of Kii Peninsula, Japan (34°13.31'N, 136°42.41'E–34°13.31'N, 136°42.97'E) during the daytime (1525–1531) on 27 November 2018. The gear was towed along the bottom for 5 min at a speed of 2 knot by TRV Seisui-maru, Mie University. Soon after collection, the gill cavity of the host was examined under a binocular lens. Three pairs of the parasitic copepods were fixed in 10% neutralized formalin/sea-water and two pairs in 99.5% ethanol. The whole bodies and appendages of the dissected copepods were mounted on Humes and Gooding's (1964) slides in a few drops of lactophenol, examined under a microscope (Olympus BX53), and illustrated with the aid of a drawing-tube attached to the microscope.

Terminology follows Ho (1970), Ho and Dojiri (1988) and Huys and Boxshall (1991). The host fish identification was based on Nakabo and Doiuchi (2013). The type specimens and host fish are deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT-Cr and NSMT-P, respectively).

TAXONOMY

Subclass Copepoda Milne Edwards, 1840
Order Cyclopoida Burmeister, 1834
Family Chondracanthidae Milne Edwards, 1840
Genus *Lagochondria* Ho and Dojiri, 1988

Remarks. The chondracanthid genus *Lagochondria* was monotypic before the discovery of the new species described below, and originally defined as follows (Ho and Dojiri, 1988): female: (1) the head region consisting of the cephalosome only, (2) head with a pair of antero-dorsally directed processes, (3) the neck short, comprising the first pedigerous somite, (4) the trunk with a pair of divergent posterior processes, (5) genital complex and abdomen almost completely fused, (6) caudal ramus bearing three basal setae, (7) egg sac, cylindrical with a multiseriate arrangement of eggs, (8) antennule modified, claviform, (9) antenna unciniate, with an atrophied tip, (10) legs 1 and 2 biramous, indistinctly segmented; male: (1) body less modified, (2) the first and second pedigerous somite not fused to the cephalosome, (3) the abdomen differentiated from the genital complex, (4) caudal ramus with four basal setae, (5) the antennule 2-segmented, with thick basal and slender terminal segments, (6) the antenna unciniate, with an atrophied tip, (7) legs 1 and 2 biramous.

The new species is easily distinguished from the type

species *L. nana* by the morphology of the neck and trunk of the female, but other gross morphological features of the female and the male morphology are essentially shared diagnostic features with the type species. Therefore, some parts of the diagnosis should be emended as follows: the female trunk with or without a pair of posterolateral lobes; caudal ramus of female armed with three or four basal setae.

***Lagochondria quadrata* Ohtsuka and Nitta, n. sp.**
(Figs. 1–4)

Types. All type specimens found from gill cavity of male *Repomucenus virgis* (total length 50.8 mm; standard length 39.3 mm) (NSMT-P 134291) collected at depth of 82 m off Kii Peninsula, Japan (34°13.31'N, 136°42.41'E–34°13.31'N, 136°42.97'E) during the daytime (1525–1531) on 27 November 2018. Holotype: one ovigerous adult female, whole specimen (NSMT-Cr 26303). Allotype: adult male attached to holotypic adult female, whole specimen (NSMT-Cr 26304). Paratypes: adult female, dissected, mouthparts and legs on two glass slides, body in vial (NSMT-Cr 26305) and adult male clinging to this paratypic adult female, dissected, body and appendages on glass slide (NSMT-Cr 26306); ovigerous adult female, whole specimen (NSMT-Cr 26307) and adult male clinging to it (NSMT-Cr 26308). Copepodid IV female, whole specimen (NSMT-Cr 26309) and copepodid IV male clinging to it, whole specimen (NSMT-Cr 26310); copepodid V female, whole specimen (NSMT-Cr 26311) and copepodid V male detached from it (NSMT-Cr 26312).

Adult female. Body (Fig. 1A–D) consisting of cephalosome, short neck, massive trunk, and short genital complex and abdomen. Total lengths of three type specimens, measured from cephalic process to posterior end of caudal rami excluding terminal element, 1.51, 1.46 and 1.69 mm (holotype 1.51 mm). Cephalosome ca. 1.4 times as wide as long (excluding cephalic process), trapezoidal, located at angle of about 135° to trunk. Mouth protruded ventrally (Fig. 1B, D). Cephalic processes (Fig. 1A–D) recurved basally, directed anterodorsally. Neck (Fig. 1B, D) very short, distinctly constricted between parts bearing legs 1 and 2, more or less flexible due to constriction of muscles. Trunk (Fig. 1A–D) about three times as long as cephalosome, squared outline in dorsal view, massive, lacking posterolateral processes as present in type species *L. nana* (see Ho and Dojiri, 1988, figs 30, 31); in dorsal view, slightly asymmetrical; in lateral view, ventral trunk margin sinuate in holotype (Fig. 1B); somewhat variable in thickness, due to development of ovary and internal eggs. Genital complex separate from short abdomen (Fig. 1E): paired gonopores located ventrolaterally; abdomen hemispherical, terminating in paired, slender caudal rami. Caudal rami (Fig. 1E, F) with swollen basal part bearing 4 fine setae and slender distal part with small terminal seta whose base incompletely fused to segment. Egg sacs (Fig. 1A, B) paired, with multiseriate arrangement of eggs.

Antennule (Fig. 2A) claviform; setal group formula following Ho and Dojiri (1988), 2, 1, 3, 1, 2, 3, 6+aesthetasc; two terminal setae with common base. Antenna (Fig. 2B, C) 2-segmented, proximal segment heavily sclerotized, with minute seta; distal segment strongly curved claw plus offset

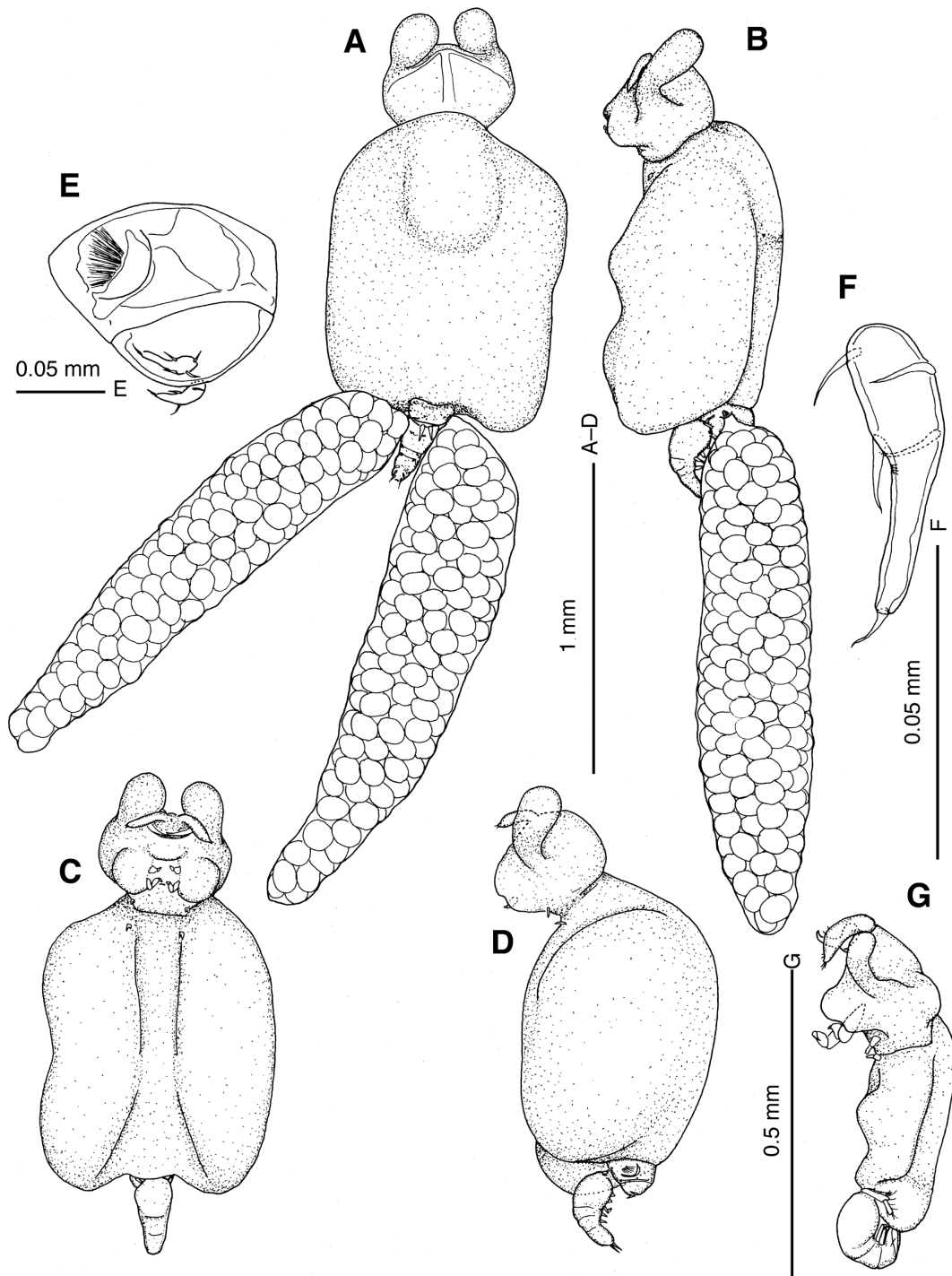


Fig. 1. *Lagochondria quadrata*, female, holotype adult female with attached allotype adult male (A–C), paratype adult female with attached paratype adult male (D–F), fourth copepodid female with attached paratype fifth copepodid male (G). (A) Habitus, dorsal view; (B) Habitus, lateral view; (C) Habitus, ventral view; (D) Habitus, lateral view, egg sacs omitted; (E) Urosome, egg sacs and adult male omitted ventrolateral view; (F) Caudal ramus; (G) Habitus, lateral view.

atrophied tip bearing one subterminal and two terminal setae and terminal rounded knob. Labrum (Fig. 2D) concave along mid posterior margin. Mandible (Fig. 2D, E) serrate along both sides of falcate process. Maxillule (Fig. 2D, F) unilobed, with two minute setae subterminally and two thick, short setae terminally and minute setule subterminally. Maxilla (Fig. 2D, G) 2-segmented, first segmented heavily sclero-

tize, unarmed, second segment sharply pointed into hook, with two relatively long slender setae basally. Maxilliped (Fig. 2D, H) 3-segmented; first segment unarmed; second segment located at right angle to preceding segment, with patch of minute prominences at inner distal corner; third segment curved inward, with inner accessory process at mid-length.

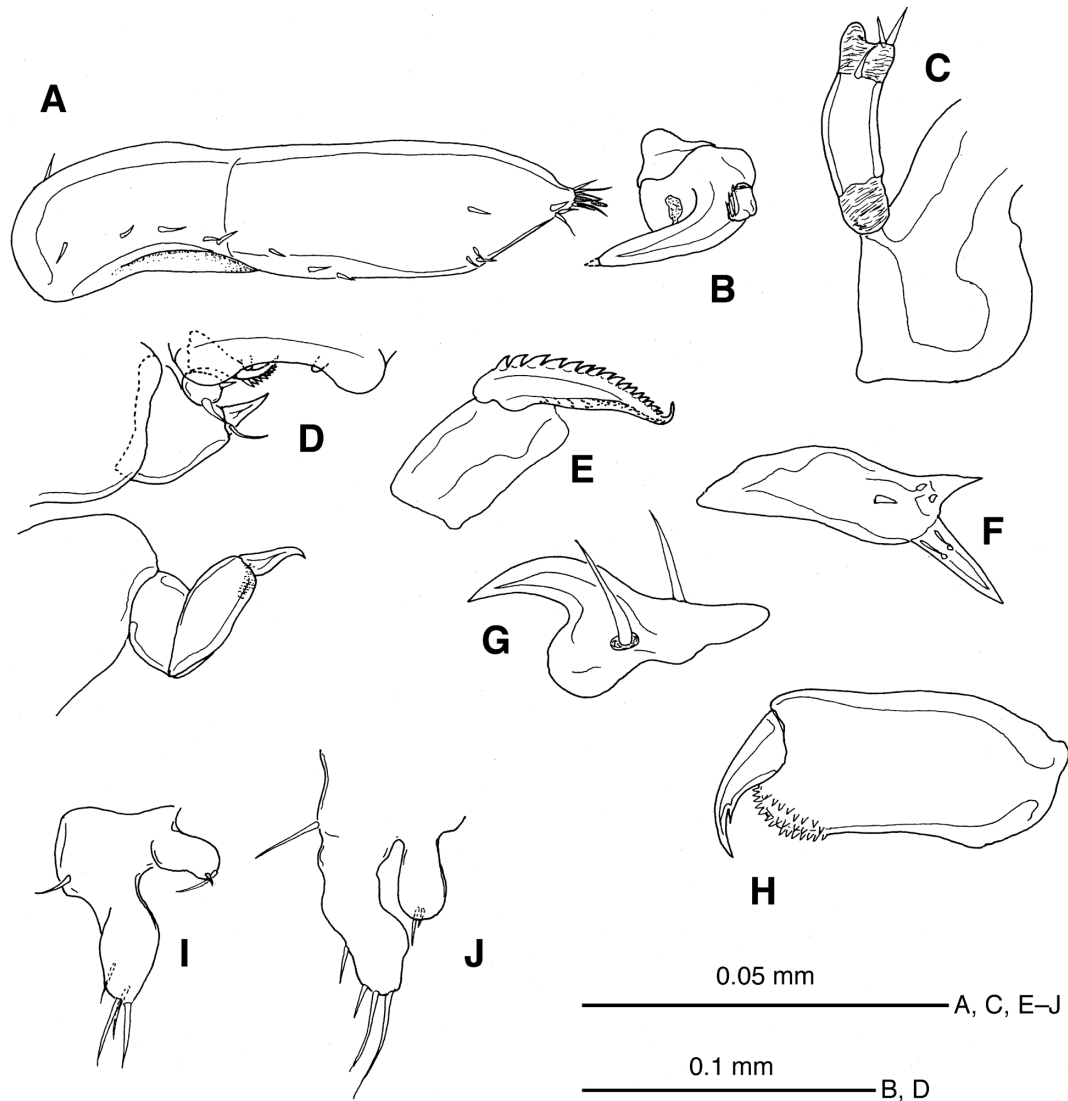


Fig. 2. *Lagochondria quadrata*, adult female, paratype. (A) Antennule; (B) Antenna; (C) Atrophied tip of antenna; (D) Mouthparts, ventral view, *in-situ*; (E) Mandible; (F) Maxillule; (G) Distal segment of maxilla; (H) Second and third segments of maxilliped; (I) Leg 1; (J) Leg 2.

Legs 1 (Fig. 2I) and 2 (Fig. 2J) reduced, biramous; segmentation indistinct; setal formula of both legs as follows: protopod with 1 outer seta; exopod and endopod bearing four and two setae, respectively

Adult male. Allotype and two paratype males located on ventral side of genital complex of females, clinging on using prehensile antennae (Figs. 1A–F, 3). Body (Fig. 3A) consisting of cephalosome, two pedigerous somites and urosome, indistinctly segmented, with suture lines visible between pedigerous somites; 0.35, 0.35 mm in length ($n = 2$), measured from anterior margin of cephalosome to posterior tip of caudal ramus including terminal element Rostrum triangular, jointed at base (not illustrated). Caudal ramus (Fig. 3B) tapering distally, bearing three inner and two outer setae along margin; terminal seta inserted into socket-like structure.

Antennule (Fig. 3C) 2-segmented; proximal segment thick, protruded anterodistally; setal group formula following Ho and Dojiri (1988), 1, 2, 1, 2, 1, 1, 1, 3, 2; distal segment slender, setal group formula of 4, 3, 7+ae. Antenna (Fig. 3D)

2-segmented, proximal segment heavily sclerotized, with minute seta; distal segment strongly curved claw with offset atrophied tip bearing four stout, hook-like setae and one minute seta; aesthetasc-like element and tiny seta on knob present at inner base of hook. Labrum (Fig. 3E) oval, with four secretory openings along posterior margin. Mandible (Fig. 3E) similar to that of female, bearing at least 18 and 15 teeth on convex and concave sides, respectively. Maxillule (Fig. 3E) small, bearing one long terminal, one subterminal, and one minute setae along inner margin. Maxilla (Fig. 3E) 2-segmented, heavily sclerotized; proximal segment unarmed; distal segment strongly curved inward, hook-like, with 2 setae of unequal lengths basally and serrations along inner distal margin. Maxilliped (Fig. 3F) 3-segmented, unarmed; distal segment, hook-like.

Legs 1 (Fig. 3G) and 2 (Fig. 3H) reduced, biramous; segmentation indistinct except for junction between basis and exopod; intercoxal sclerite present; coxa and basis incompletely fused with suture line visible; basis with fine seta at outer corner. Leg 1 with setal formula of exopod and endo-

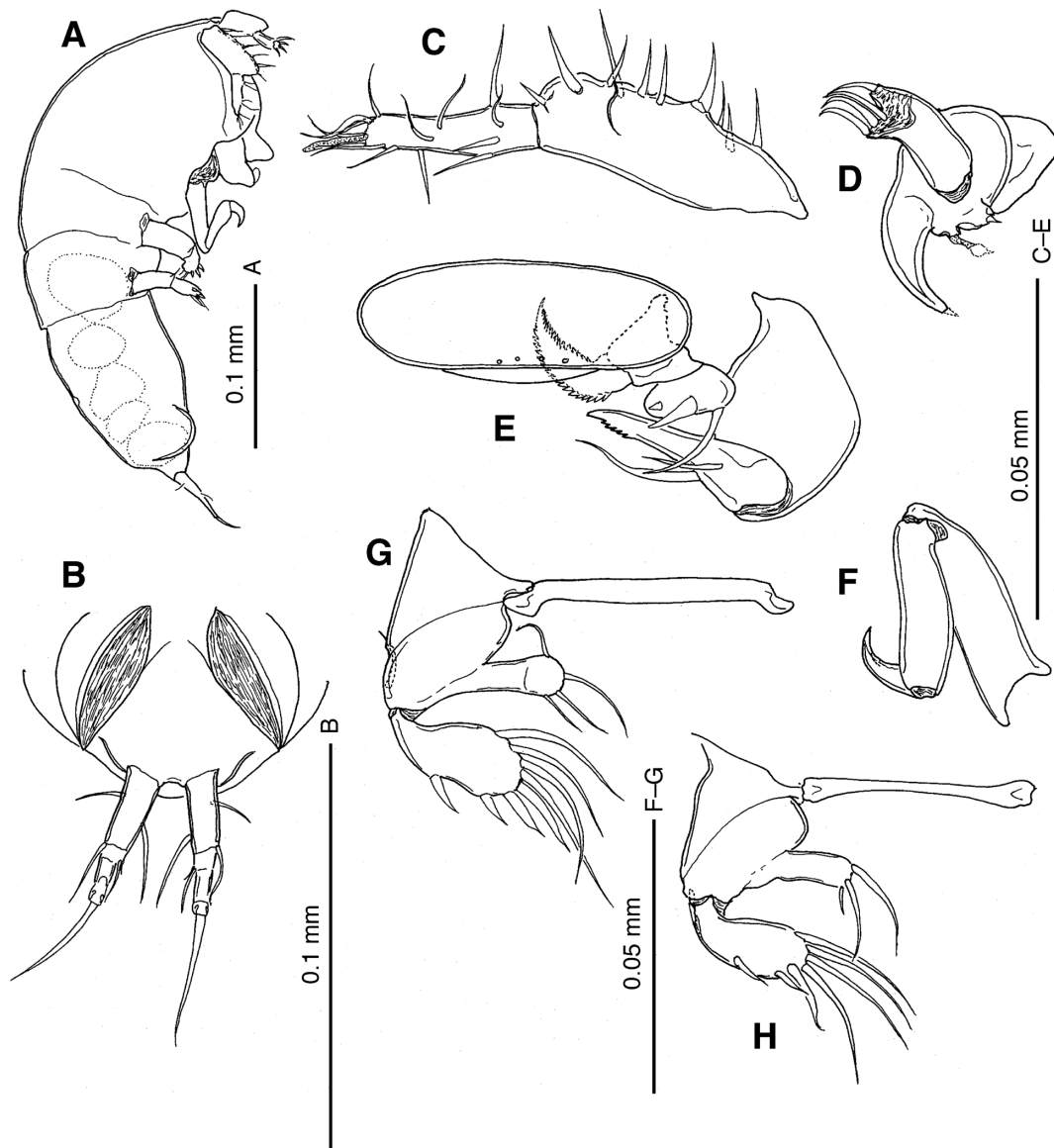


Fig. 3. *Lagochondria quadrata*, male, paratype. (A) Habitus, lateral view; (B) Genital area and caudal rami; (C) Antennule; (D) Antenna; (E) Mouthparts; (F) Maxilliped; (G) Leg 1; (H) Leg 2.

pod of III, I, 4 and 4 and II, I, 4 and 3, respectively.

Remarks. The female of the new species is easily distinguished from *L. nana* by comparison of the habitus: (1) trunk square in outline in dorsal view and lacks paired posterior processes (cylindrical, with paired posterior processes in *L. nana*); (2) the neck is very short, so the distance between the legs is less than one-tenth the length of the body (ca. 0.15). The appendages of *L. quadrata* are essentially similar to those of *L. nana*, but differ in the number and size of various setal elements and in the relative lengths of segments: (1) the female antennular setal group formula following Ho and Dojiri (1988), 2, 1, 3, 1, 2, 4, 3, 6+aesthetasc (2, 1, 3, 1, 1, 4, 3, 7 (one of them may be an aesthetasc) in *L. nana*); (2) the atrophied tip of the antenna armed with three setae (4 or 5); (3) legs 1 and 2 with four and two setae on the exopod and endopod, respectively (6, 2 and 5, 4, respectively). In addition, in the new species, the terminal caudal seta was incompletely separated from the segment, while in *L. nana*,

it is completely fused to the segment to form a "setiform distal portion" (Ho and Dojiri 1988). In the male, the new species is readily differentiated from *L. nana* by the structure of the caudal rami and legs: (1) the caudal ramus with three medial setae and terminal seta socketed to base (two setae and terminal elements fused to caudal rami); (2) endopod of leg 1 having 4 setae (three setae).

The general body forms of both sexes of the new species resemble those of *Prochondracanthopsis quadricornutus* Shiino, 1960 (= *Humphreysia hoi* Do and Kasahara, 1982) parasitizing the gobiid, *Suruga fundicola* Jordan and Snyder, 1901, and the pinguipedids, *Paraperca sexfasciata* (Temminck and Schelegel, 1843) and *P. multifasciata* Doderlein, 1884 (Shiino, 1960; Do and Kasahara, 1982; Ho et al., 2011), but the latter shows remarkable reductions in the setation in the female antennule and male maxilliped, and in the segmentation and setation of legs of both sexes (see Do and Kasahara, 1982; Ho et al., 2011) than those of

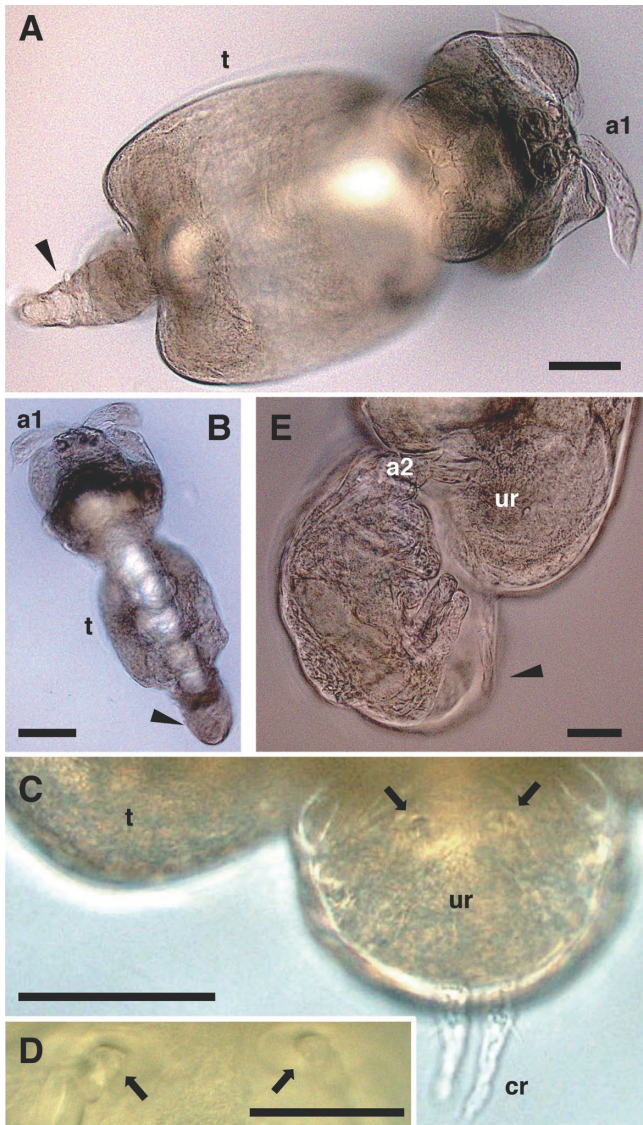


Fig. 4. Precopulatory mate guarding and nuptial organs in *Lagochondria quadrata*. (A) Pair of fifth copepodid female and fifth copepodid male (indicated by arrowhead), ventral view; (B) Pair of fourth copepodid female and fourth copepodid male (indicated by arrowhead), ventral view; (C) Urosome of fifth copepodid female (A), ventral view, note nuptial organs (arrowed); (D) Nuptial organs (arrowed) of fifth copepodid female (A), ventral view; (E) Fourth copepodid male (indicated by arrowhead) clinging to urosome of fourth copepodid female (B), lateral view, grasping points by antenna. a1: antennule; a2: antenna; cr: caudal ramus; t: trunk; ur: urosome. Scales = 0.1 mm (A–C); 0.05 mm (D, E).

L. quadrata n. sp.

Precopulatory mate guarding. All three adult females were each accompanied by an adult male on the ventral side of the genital complex. Late copepodid stages of the female were also found on the same host fish. These specimens were tentatively identified as the fifth (Fig. 4A; body length 0.73 mm) and fourth (Fig. 4B, body length 0.53 mm) copepodid stages, by reference to Izawa (1986) who provided a full description of all copepodid stages of the chondracanthid *Acanthocondria yui* Shiino, 1964. The fourth (Fig. 4B, E, body length 0.29 mm) and fifth (Fig. 4A, 0.38 mm) copepo-

did males each clung onto the urosome of a female copepodid at stage IV and V, respectively, with the antennae (arrows in Fig. 4E), and in both of these the gonopores were not open. This can be regarded as a kind of precopulatory mate guarding, which is widely found in cyclopoid and siphonostomatoid copepods (Boxshall, 1990; Itoh and Nishida, 2008; Ismail et al., 2013; Ijichi et al., 2017). In parasitic cyclopoid copepods, precopulatory mate guarding was exclusively known from families associated with benthic invertebrates such as cnidarians, polychaetes and molluscs (Huys et al., 2006; Itoh and Nishida, 2008; Ichiji et al., 2017). The present discovery is the first record of precopulatory mate guarding in any cyclopoid family parasitic on fish hosts. In addition, a combination between the late copepodid stages of both sexes is unique for precopulatory mate guard.

A pair of nuptial organs was found on the antero-ventral side of the fifth copepodid female (Fig. 4C, D).

Etymology. The new specific name is derived from the Latin “*quadratus*” meaning squared, and alludes to the squared outline of the trunk of the female.

ZooBank registration. urn:lsid:zoobank.org:act:764A310A-C4E8-41FD-AF7F-2BCD1491B051.

DISCUSSION

Precopulatory mate guarding

Boxshall (1990) reviewed precopulatory mate guarding in podoplean copepod orders. In the Cyclopoida, Harpacticoida and Siphonostomatoida, precopulatory mate guarding between an adult male and the first or second to sixth copepodid stages of a female was commonly observed (Boxshall, 1990; Ismail et al., 2013; Ijichi et al., 2017). Itoh and Nishida (2008) summarized this mating behavior in “poecilostomatoid” copepods associated with marine invertebrates, and found some distinct relationships of reproductive strategies among precopulatory mate guarding, low sex-ratio (percentage of male) and male polymorphism. Interestingly, they found the presence or absence of this behavior even between two species of the cyclopoid genus *Hemicyclops* loosely associated with marine benthic invertebrates. In *H. spinulosus* Itoh and Nishida, 1998 with small populations, precopulatory mate guarding was found, but not in *H. gomsoensis* Ho and Kim, 1991 with large populations, suggesting that the behavior may be more evolutionarily beneficial to “males in securing mates in low-density populations” (Itoh and Nishida, 2008). In addition, Ijichi et al. (2017) found very distinct relationships between precopulatory mate guarding and the different attachment sites by the cyclopoid *Goidelia japonica* Embleton, 1901 on its echiuran host. This behavior was exclusively exhibited in the echiuran rectum, in which adult males and copepodids were predominant, but not on the host body surface on which only adult males and ovigerous and non-ovigerous females occurred. Ijichi et al. (2017) hypothesized that this behavior may guarantee the retention of small-sized copepodids in the host rectum, and that in the rectum, due to much higher abundance of adult males compared with that of copepodids, sperm competition may be severe.

In case of *Lagochondria quadrata* n. sp., not only its low-density populations but also another above-mentioned feature is supposed to be related to evolutionary advantage

for the retention of precopulatory mate guarding. The adult and the fourth/fifth copepodid dwarf males each clinging to adult and copepodid females receive nutrition from secretions produced by the female via her paired nuptial organs (Østergaard, 2004; Østergaard and Boxshall, 2004). This hypothesis is supported by the presence of paired nuptial organs on the ventral side of the urosome of the fifth copepodid female (see Fig. 4C, D). Those of adult and the fourth copepodid females could not be confirmed, partly because we did not want to detach all the males from their associated females, and partly because it was difficult to detect the presence of the organ in the dissected paratypic adult female. However, the organs are most likely held by these stages of females. It is unknown whether earlier copepodid stages show precopulatory mate guarding.

Zoogeography

The present discovery extends the distributional range of the genus *Lagochondria* from Australia to Japan, although the host-specificity is conservatively limited to the Callionymidae. According to Boxshall and Halsey (2004), the host-specificities of most of chondracanthid genera are so high as to be restricted to one or a few families of fish hosts except for some genera such as *Acanthochondria*, *Chondracanthus*, *Heterochondria*, and *Pharodes* that parasitize more than five host families. Paterson and Poulin (1999) inferred that species of the genus *Chondracanthus* exhibit a distinct co-evolutionary trend with the host fish, and that host-switching was very rare. Since the family Callionymidae have a wide distribution in the Indo-Pacific

and Atlantic oceans (Nakabo, 1982), *Lagochondria* and its relatives are likely to be discovered from more widely across the world oceans, particularly from the Indo-West Pacific. The occurrence of parasitic copepods has scarcely been reported from callionymids, presumably due to the paucity of investigation (El-Rashidy and Boxshall, 2012). Those authors reviewed the parasitic copepod fauna from callionymids in the world, and inferred that more taxa would be found from this host family. The following species are so far recorded: four species of the Chondracanthidae; at least six species of the Pennellidae; one species of each the Lernanthropidae, Lerneopodidae and Taeniacanthidae (El-Rashidy and Boxshall, 2012).

Ho and Dojiri (1988) pointed out that the following chondracanthid genera in the Chondracanthidae exhibit a relatively primitive state in the retention of an atrophied tip of the antenna: *Lagochondria*, *Humphreysia*, *Immante*, *Neobranchiochondria*, *Praecidochondria*, *Protochondria*, and *Pseudacanthocanthopsis*. *Lagochondria* and *Pseudacanthocanthopsis* are shown as early divergences from the main chondracanthid lineage in the phylogenetic trees generated by Østergaard et al. (2003). In addition, all these genera, other than *Protochondria*, occurring in the East Pacific, are distributed across the West Pacific (Ho and Dojiri, 1988) (Fig. 5). Notably, these are restricted to the West Pacific without extending into the Indian Ocean.

Fleminger (1986) proposed a hypothesis that speciation of an Indo-West Pacific planktonic copepod species group, *Labidocera pectinata* Thompson and Scott, 1903 group could have been enhanced by vicariant events, such as eustatic changes and upwelling during the Pliocene to Pleistocene. Since, in that species group, some species have a restricted distribution in the West Pacific, a similar evolutionary pattern may be applicable to the distribution of these chondracanthids. In particular, separate distributions of the same congeners such as *Lagochondria* spp., *Praecidochondria* spp., and *Pseudacanthocanthopsis* spp. in the North and South Pacific may be explained by Fleminger's (1986) hypothesis. The main host fish families for these genera are summarized by Boxshall and Halsey (2004), but no general co-evolutionary trend can be found. Since Østergaard et al.'s (2003) phylogenetic analysis of the family Chondracanthidae points out topographic incongruities between trees based on characters of either the females or the

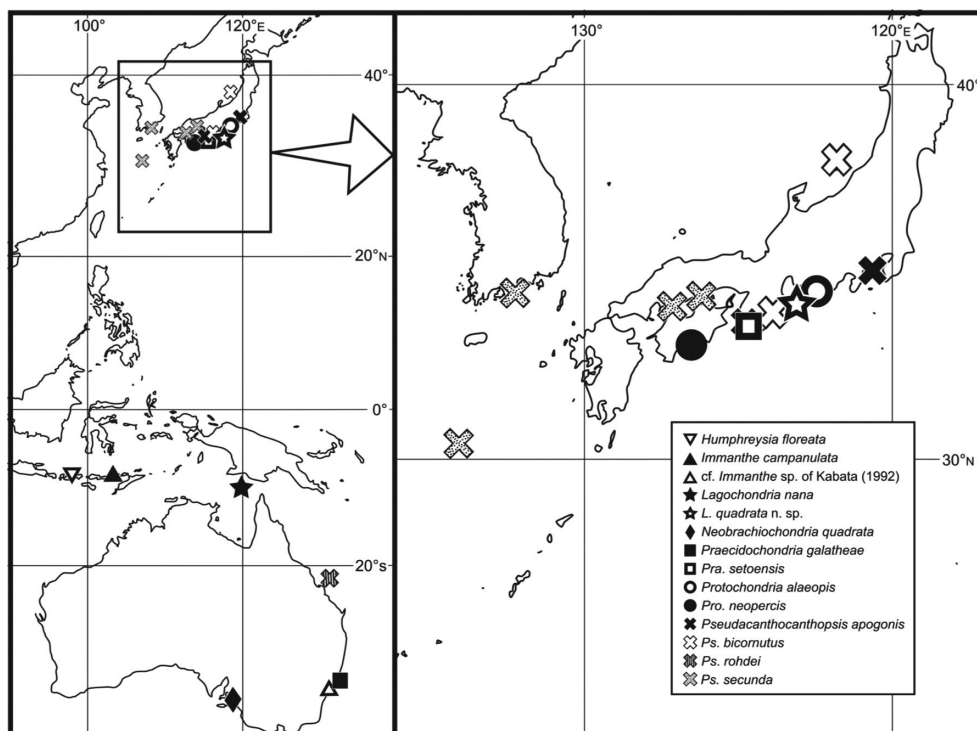


Fig. 5. Distribution of chondracanthids exhibiting atrophied tip on the antenna of adult females, excluding *Protochondria longicauda* Ho, 1970 occurring in the West Pacific (Ho, 1970). The distribution records were collated from Kabata (1969, 1992), Ho (1970), Ho and Dojiri (1976, 1988), Venmathi Maran et al. (2013), and Nagasawa et al. (2013).

males, a new genetic analysis is necessary to unravel the evolutionary relationships of these lineages of chondracanthids. At the familial level, Huys et al. (2006) proposed on the basis of a molecular analysis using 18S rDNA that the family Chondracanthidae comprises a member of the superfamily Lichomolgoidea with Anchimolgidae, Lichomolgidae, Pseudacanthessidae, Rhynchomolgidae, Sabelliphilidae and Xarifiidae, but at the generic level, no study has been conducted.

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