



Lomanotocola nishiharai n. sp., a New Species of Copepod Parasitic on the Facelinid Nudibranch, Sakuraeolis enosimensis (Baba, 1930), from the Seto Inland Sea, Western Japan, Including Histological Observations of the Female Lateral Body Process

Authors: Uyeno, Daisuke, and Hirose, Euichi

Source: Zoological Science, 35(4) : 382-387

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zs180006>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

***Lomanotricula nishiharai* n. sp., a New Species of Copepod Parasitic on the Facelinid Nudibranch, *Sakuraeolis enosimensis* (Baba, 1930), from the Seto Inland Sea, Western Japan, Including Histological Observations of the Female Lateral Body Process**

Daisuke Uyeno^{1*} and Euichi Hirose²

¹Graduate School of Science and Engineering, Kagoshima University, 1-21-35 Korimoto, Kagoshima 890-0065, Japan

²Department of Chemistry, Biology and Marine Science, Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

Splanchnotrophidae Norman and Scott, 1906 is a family of parasitic copepods that infest nudibranchian and sacoglossan sea slugs. In this study, a new species of splanchnotrophid copepod, *Lomanotricula nishiharai* n. sp., is described based on specimens of both sexes collected from the facelinid nudibranch, *Sakuraeolis enosimensis* (Baba, 1930), in the Seto Inland Sea off Hiroshima, central Japan. It represents the third species of *Lomanotricula* Scott and Scott, 1895 and is characterized by the following female characters: the cephalosome distinctly protruded; the second and third lateral processes on the body originated from same bases; the caudal rami bears a seta V which almost same as long as the rami. Ultrastructural observations revealed that the cuticular surface of the lateral process on the female body is covered with numerous protuberances that may have protective functions against the cellular immune system of the host.

Key words: parasitic copepods, Splanchnotrophidae, *Splanchnotrophus*, *Lomanotricula*, Nudibranchia, ultrastructure, cuticular layer, ovary

INTRODUCTION

Members of the family Splanchnotrophidae are bizarre, highly transformed endoparasitic copepods that infest nudibranchian and sacoglossan sea slugs (e.g., Huys, 2001; Boxshall and Halsey, 2004; Anton et al., 2016). Although their prevalence in the hosts typically display a seasonal range, several reports have indicated that infection rates can sometimes reach 100% (Schrödl, 2002; Abad et al., 2011). There are several records of negative impacts on hosts caused by copepods, e.g., atrophy of gonads, growth inhibition of organs, damage to digestive organs, and death (Marshall and Hayward, 2006; Wolf and Young, 2014). The family was originally established based on *Splanchnotrophus* Hancock and Norman, 1863 by Norman and Scott (1906) and subsequently saw the addition of several highly transformed genera, some of doubtful affinity. Huys (2001) recognized three valid genera, i.e., *Splanchnotrophus* with four valid species, *Ismaila* Bergh, 1867 with three valid species, and *Lomanotricula* Scott and Scott, 1895 with two valid species and established two new monotypic genera, *Arthurius* Huys, 2001 and *Ceratosomicola* Huys, 2001. Eleven spe-

cies of *Ismaila*, four species of *Ceratosomicola*, two species of *Arthurius*, and two species of *Splanchnotrophus* have been added since Huys' (2001) revision of the family (Haumayr and Schrödl, 2003; Salmen et al., 2008a, b; Uyeno and Nagasawa, 2012; Anton et al., 2016). In addition, the genus *Majimun* Uyeno and Nagasawa, 2012 was proposed for a single species from Japanese waters (Uyeno and Nagasawa, 2012). Currently, the family contains 31 species in six genera, all of which occur in temperate to tropical regions.

In this study, a new species of *Lomanotricula* is described based on unique morphological characters of both sexes collected from the Seto Inland Sea, Japan. The internal morphology and cuticular ultrastructures of the lateral processes on the body of female were observed based on histological and ultrastructural approaches.

MATERIALS AND METHODS

Sampling and microscopy

Nudibranchs were collected using SCUBA diving in coastal waters of the Seto Inland Sea off Hiroshima, central Japan. Copepods were carefully dissected from the body cavities of their hosts using forceps and scissors under a stereomicroscope and were then fixed in 80% ethanol. The copepods were subsequently soaked in lactophenol for about 24 h, dissected with sharpened tungsten needles, and examined using a modified version of the

* Corresponding author. E-mail: duyeno@sci.kagoshima-u.ac.jp
doi:10.2108/zs180006

wooden slide method of Humes and Gooding (1964) under a compound microscope. Drawings were made with the aid of a drawing tube. The copepod body parts were measured using an ocular micrometer and measurements are given in millimeters (mm). The body length was measured from the anterior margin of the rostral area to the posterior margin of the caudal rami. Type specimens are deposited in the crustacean collection of the National Museum of Nature and Science, Tsukuba (NSMT), Japan.

Histological and ultrastructural observations

For observation of internal structure and ultrastructures of the copepod integument, the distal part of the first lateral process was cut from a freshly collected adult female (NSMT-Cr 26848), fixed in 2.5% glutaraldehyde, 0.1 M cacodylate, and 0.45 M sucrose, and stored at 4°C. The process was subsequently rinsed in 0.1 M cacodylate and 0.45 M sucrose and post-fixed for 1.5 h in 1% osmium tetroxide and 0.1 M cacodylate. It was then dehydrated through a graded ethanol series, cleared with *n*-butyl glycidyl ether, and embedded in Agar Low-viscosity Resin (Agar Scientific, England). Thick sections were stained with toluidine blue for histological observation under a light microscope. Thin sections were stained with uranyl acetate and lead citrate and examined using a transmission electron microscope (TEM: JEM-1011, JEOL, Japan).

RESULTS

Systematic account

Family **Splanchnotrophidae** Norman and Scott, 1906
 Geus **Lomanoticola** Scott and Scott, 1895

Lomanoticola nishiharai n. sp.
 (Figs. 1–3)

Type material. Holotype: adult female (NSMT-Cr 26845), ex body cavity of *Sakuraeolis enosimensis* (Baba, 1930) (Nudibranchia: Facelinidae), off Irukabana, Nohmi-jima Island, Hiroshima, Seto Inland Sea (34°13'49"N, 132°23'7"E), 10 m, 14 February 2014. Allotype: adult male (NSMT-Cr 26846), collection data same as that for holotype. Paratypes: 1 adult male (NSMT-Cr 26847), collection data same as that for holotype; 2 adult females (NSMT-Cr 26848), ex body cavity of *S. enosimensis*, off Irukabana, Nohmi-jima Island, Hiroshima, Seto Inland Sea (34°13'49"N, 132°23'7"E), 10 m, 15 February 2014.

Morphology of holotype adult female. Body (Figs. 1D, 2A) 2.26 long. Prosome (Fig. 2A, B) composed of anterior region (cephalosome), middle region (first to second pedigerous somites), and posterior region (third and fourth pedigerous somites). Cephalosome (Fig. 2A, B) broad, not elongate. Middle region (Fig. 2A, B) large, bearing three pairs of long, conical lateral processes and pair of spherical posterolateral processes; lateral processes (Fig. 2A) conical, curved, and as long as or slightly shorter than body; bases of third lateral processes situated on same part of that of second lateral processes. Posterior region (Fig. 2A–C) small, without armature.

Urosome (Fig. 2A–C) small, composed of genito-abdomen (Fig. 2D) bearing pair of round lateral lobes, unarmed opercula, and ventral genital apertures. Caudal rami (Fig. 2E) small, almost as long as wide, bearing five setae, single conical element and single spiniform dorsal process; apical seta (seta V) long, setose.

Antennule (Fig. 2H) Two-segmented; proximal segment bearing two blunt spines; terminal segment with transverse constriction, armature consisting of two blunt spines and three setae in proximal part and nine setae and two aesthetascs in distal part. Antenna (Fig. 2I, J) Three-segmented; coxo-basis broad, bearing spine at inner distal corner; proximal segment of endopod bearing inner spine; distal segment of endopod tapering into strong apical claw, with four elements. Labrum (Fig. 2I) bilobate, with flat surface. Mandible (Fig. 2I, K) tapering into single curved, spatulate blade with four dentiform processes. Paragnath (Fig. 2I) represented by pinnate lobe; intermaxillary swelling with two spinular patches. Maxillule not observed. Maxilla (Fig. 2I, L) Two-segmented; syncoxa unarmed; allobasis with spiniform apical element and lateral seta. Maxilliped absent.

Leg 1 (Figs. 2B, 3A) unsegmented, weakly sclerotized and drawn out into protopod fused to elongate exopod and small endopod; protopod bearing outer basal seta; exopod drawn out into elongate lobe bearing multiple constrictions, wrinkly surface, two outer, single long apical, and two small inner elements; endopod represented by small constricted

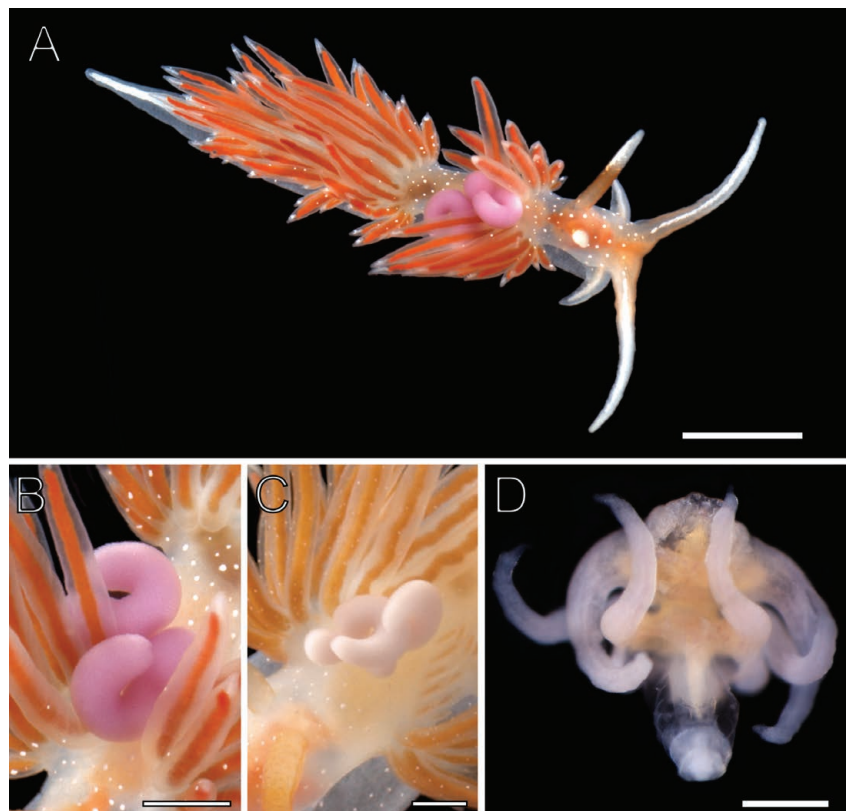


Fig. 1. Facelinid nudibranch, *Sakuraeolis enosimensis* (Baba, 1930) infested by *Lomanoticola nishiharai* n. sp. (A) Nudibranch with protruding egg sacs of copepod. (B) Egg sacs of holotype (NSMT-Cr 26845). (C) Same of paratype (NSMT-Cr 26848). (D) Live specimen of paratype (NSMT-Cr 26848), ventral. Scale bars: 3 mm (A), 1 mm (B, C), 0.5 mm (D).

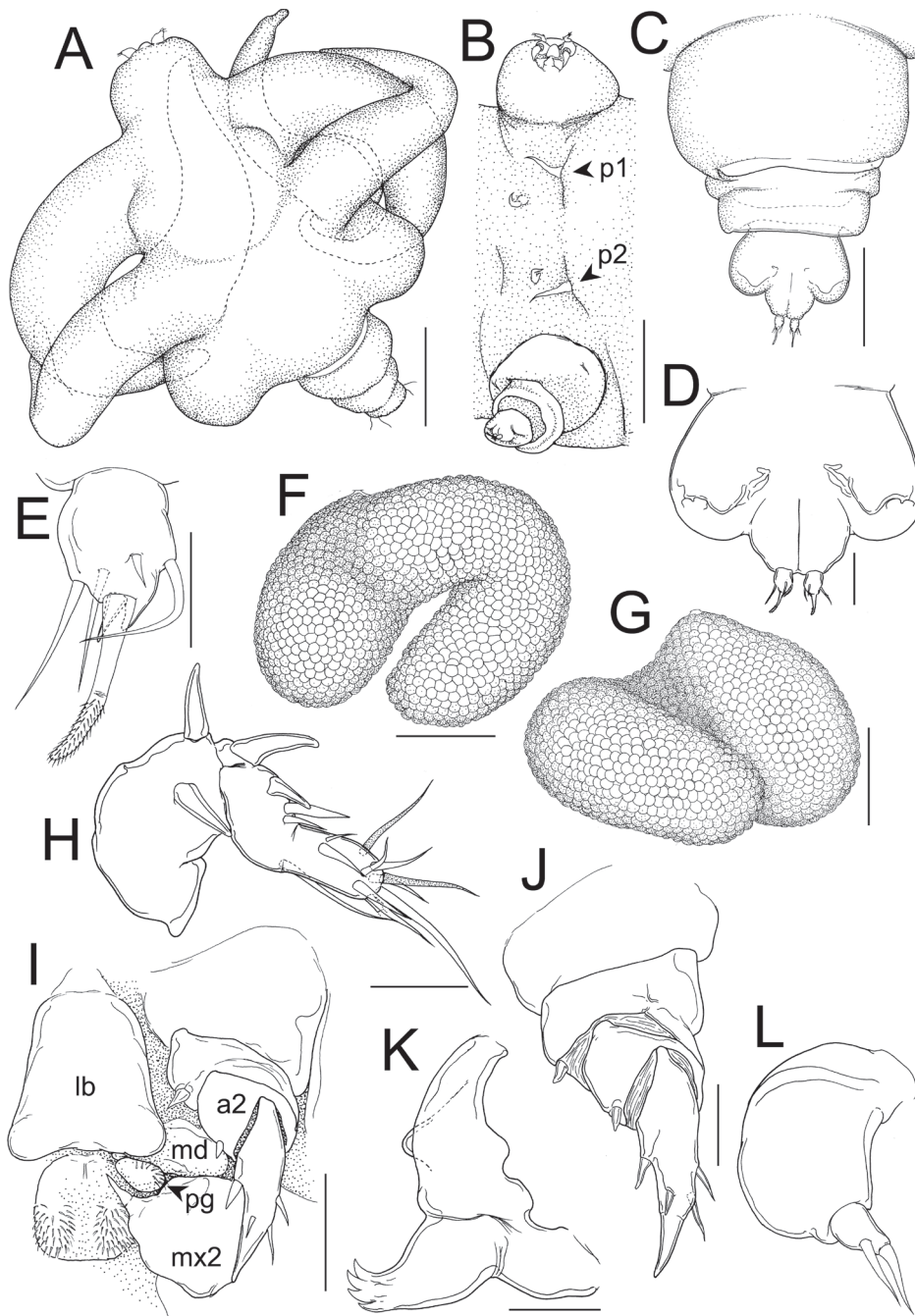


Fig. 2. *Lomanoticola nishiharai* n. sp., adult female, holotype (NSMT-Cr 26845). (A) Habitus, dorsal. (B) Midventral area of body, ventral, p1 = leg 1, p2 = leg 2. (C) Posterior portion of body, ventral. (D) Urosome, ventral. (E) Right caudal ramus, ventral. (F) Right egg sac, posterior. (G) Same, ventral. (H) Right antennule, anterior. (I) Oral area, lb = labrum, a2 = antenna, md = mandible, pg = paragnath, mx2 = maxilla. (J) Left antenna, anterior. (K) Right mandible, anterior. (L) Left maxilla, inner. Scale bars: 500 μ m (A, B, F, G), 200 μ m (C), 50 μ m (D, I), 20 μ m (E, H, L), 30 μ m (J), 10 μ m (K).

lobe bearing distal setal element. Leg 2 (Figs. 2B, 3B) unsegmented, weakly sclerotized; protopod drawn out into long exopod and small, cylindrical endopod; protopod bearing outer basal seta; exopod tapering into elongate lobe with two small outer, single long apical, and two inner small elements; round endopodal lobe unarmed. Leg 3 (Figs. 2C, 3C) represented by conical robe with apical seta, located near

posterolateral corner on ventral side of prosome.

Egg sacs (Fig. 2F, G) bilobate, bearing long curved one side and short swollen other side and attaching at about mid-length to genital apertures; color in life violet (Fig. 1A, B).

Morphology of allotype adult male. Sexual dimorphism clearly prominent in body form. Body (Fig. 3D–F) cycloform, 0.86 long. Cephalothorax (Fig. 3D–F) large, incorporating first two pedigerous somites; original boundary between cephalosome and first pedigerous somite marked by bilateral constriction posterior to maxillae. First to second pedigerous somites fused; original boundary marked by faint constriction laterally. Third and fourth pedigerous somites (Fig. 3G) free. Urosome (Fig. 3G) Two-segmented; genital somite bearing paired lateroventral apertures closed off by opercula (Fig. 3H) carrying two processes. Caudal rami (Fig. 3G, I) cylindrical, about three times as long as wide, bearing conical tip, five simple setae, and spiniform terminal seta with pinnate tip. No marked sexual dimorphism in antennule, antenna, and mouthparts (Fig. 3J). Base of antenna located anterior to labrum. Maxilliped absent.

General shape of legs 1 and 2 (Fig. 3K, L) as in female except for protopods bearing small setae; exopods tapering into sharp tip bearing several minute spiniform processes, and endopods represented by elongate, blunt lobes with small apical element. Leg 3 (Fig. 3G, M) represented by simple seta. Legs 4 and 5 absent.

Variation. The morphology of adult female paratypes ($n = 2$) is as in the holotype. The range of body length of paratypes is 1.81–2.30 (2.05 ± 0.35). Live egg sacs of paratype female pinkish white (Fig. 1C). The morphology of adult

male paratypes ($n = 1$) is as in the allotype. The body length of paratype as 0.93.

Remarks. The new species is concerned to assigned to the genus *Lomanoticola* based on the following characters of the adult female, i.e., the prosome bears lateral processes which are shorter than the body, the prosome lacks processes on dorsal or ventral sides, the presence of the

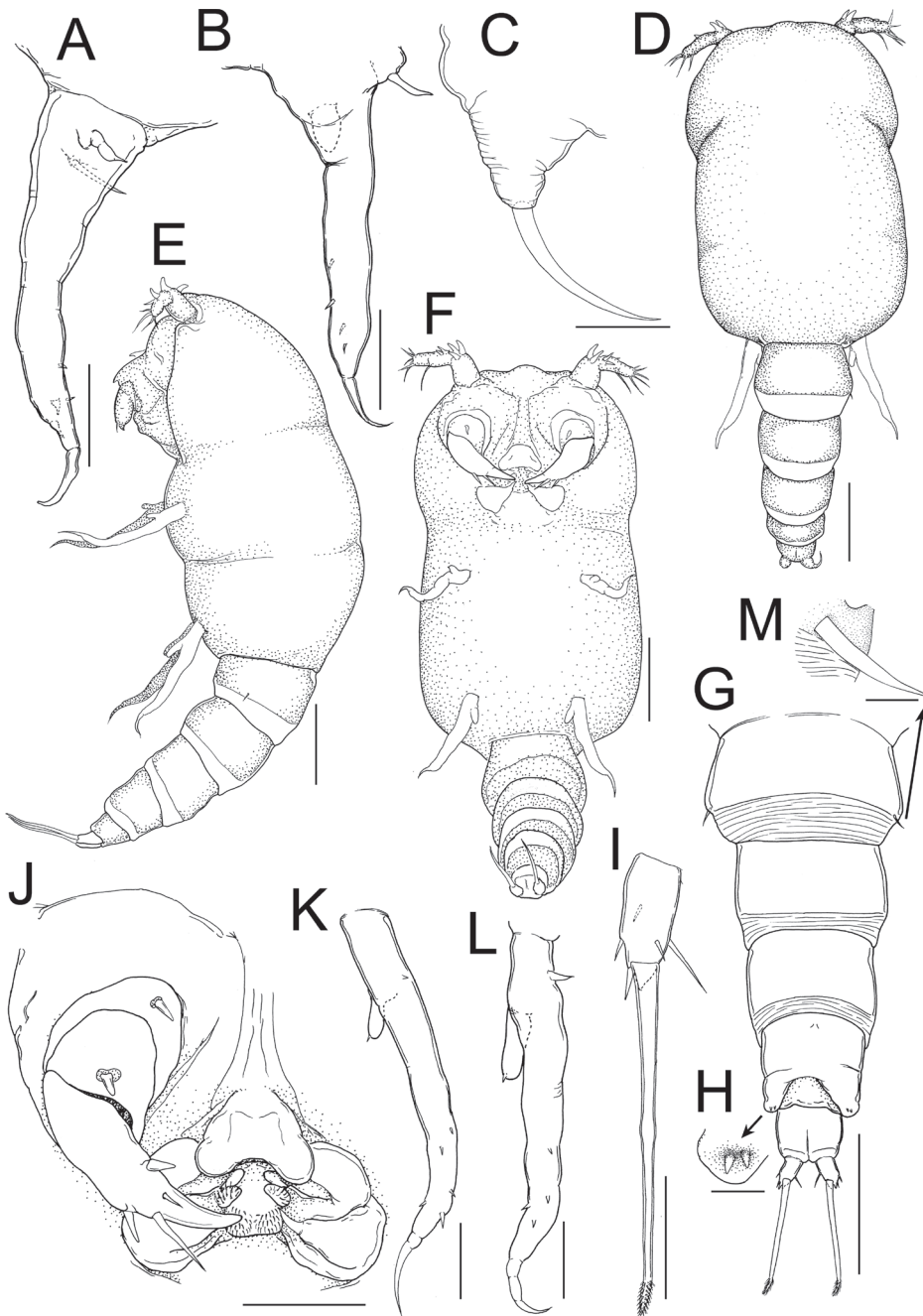


Fig. 3. *Lomanotocola nishiharai* n. sp., adult female, holotype (NSMT-Cr 26845) (A–C) and adult male, allotype (NSMT-Cr 26846) (D–M). (A) Left leg 1, inner. (B) Left leg 2, outer. (C) Right leg 3, ventral. (D) Habitus, dorsal. (E) Same, lateral. (F) Same, ventral. (G) Posterior portion of body, ventral. (H) Right genital opercula. (I) Right caudal ramus, ventral. (J) Oral area. (K) Left leg 1, outer. (L) Left leg 2, outer. (M) Left leg 3, ventral. Scale bars: 50 μm (A, B, J), 20 μm (C), 100 μm (D–G), 10 μm (H), 30 μm (I, K, L), 5 μm (M).

genito-abdomen, and the mandible represented by a curved blade (Huys, 2001; Uyeno and Nagasawa, 2012). Prior to the discovery of *L. nishiharai* n. sp. the genus contained two species are known to that are recognized as valid (Huys, 2001). The new species differs from two of these congeners, *Lomanotocola brevipes* (Hancock and Norman, 1863) and *L. insolens* Scott and Scott, 1895, by the following combination of the adult female characters: the cephalosome distinctly protruded (vs slightly projected forward); the second and

third lateral processes on the body are originated from same bases (vs the third processes attached behind of the bases of the second processes); and the caudal rami bears a seta V which almost the same length as the rami (vs. almost twice as long as the rami) (Hancock and Norman, 1863; Delamare Deboutteville, 1950).

Attachment site. Both adult females and males were found in the body cavity of the host nudibranchs. Only the posterior part of the urosome of the females and their egg sacs protruded from the host's bodies (Fig. 1A–C).

Prevalence and intensity. Three of out of total 17 nudibranchs (17.65%) collected on 14 and 15 February 2014 from the type locality were infested by one female and none or a single male.

Etymology. The specific name of the new species, *nishiharai*, was chosen in honor of Dr. Naohisa Nishihara, the director of the Satoumi Science Museum, Etajima City as a tribute to his kindness and devoted support for the senior author's fieldwork.

Newly established Japanese name for genus and species. "Ajisai-umiushi-yadori-zoku" is for the genus, and "Ajisai-umiushi-yadori" is for the new species. The color of egg sacs of the copepod is reminiscent of that of the flowers of hydrangea, called "Ajisai" in Japanese. "Umiushi-yadori" is the Japanese name for splanchnotrophid copepods.

Internal morphology and ultra-structures on integument of lateral process

The lateral processes (Figs. 1D, 2A) on the prosome were entirely embedded in the body cavity of the host. The cuticular layer, epidermis, connective tissue, and ovary were examined by histological observations (Figs. 4, 5). The thickness of the cuticular layer was not constant, ranging about 0.8–3.4 μm . The innermost (basal) part of the lateral process was occupied by the ovaries and contained eggs at different stages of development (Fig. 4).

The cuticle has a multilayered structure. The electron-dense epicuticle forms the outermost layer of the cuticle and is about 0.06–0.40 μm in thickness (Fig. 5A–C). The outer surface of the epicuticle has numerous protuberances distrib-

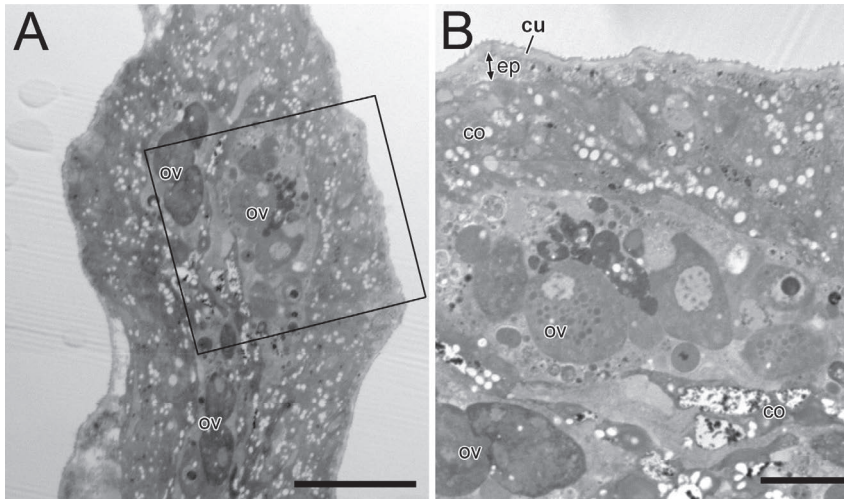


Fig. 4. Histological section of lateral process of adult female of *Lomanotocola nishiharai* n. sp. (NSMT-Cr 26848) stained with toluidine blue, cu = cuticle, co = connective tissue, ep = epidermis, ov = ovary. **(A)** Longitudinal section. **(B)** Enlargement of rectangular area in **(A)**. Scale bars: 100 μ m **(A)**, 50 μ m **(B)**.

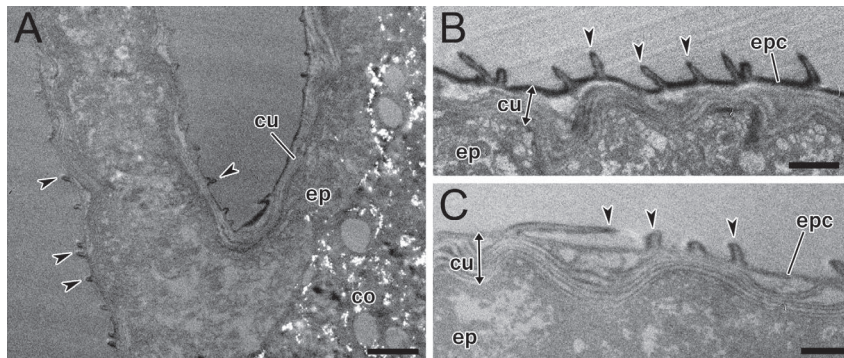


Fig. 5. Transmission electron micrographs of integument of lateral process of adult female of *Lomanotocola nishiharai* n. sp. (NSMT-Cr 26848), arrowheads indicating some of protuberances on the cuticular surface, co = connective tissue, cu = cuticle, ep = epidermis, epc = epicuticle. **(A)** Longitudinal section of apical part of lateral process. **(B)** Enlargement of cuticle lined with epidermis. **(C)** Same, another part. Scale bars: 3 μ m **(A)**, 2 μ m **(B, C)**.

uted at 1–4 μ m intervals; they are typically about 0.3–1.9 μ m in height and rarely over 4.5 μ m (Fig. 5C).

DISCUSSION

The family Splanchnotrophidae currently contains six genera. *Lomanotocola* Scott and Scott, 1895 was established based on *Lomanotocola insolens* Scott and Scott, 1895 from *Lomanotus genei* Vérany, 1846 (Nudibranchia: Lomanotidae) collected in Valentia Harbour, Ireland (Scott and Scott, 1895). The genus was relegated a junior synonym of *Splanchnotrophus* by Hecht (1895). Subsequently, Monod and Dollfus (1932) included *Splanchnotrophus* (*Lomanotocola*) *brevipes* Hancock and Norman, 1863 as the second species in the subgenus. Since *Lomanotocola* shares many characters with *Splanchnotrophus*, the validity of the genus has been discussed for a long period. The cladistic analysis based on 109 morphological characters of 24 known splanchnotrophids also supported their close relationship (Anton and Schrödl, 2013). Huys (2001) demarcated *Splanchnotrophus* from *Lomanotocola* and considered the

latter a distinct genus based on the following female characters: egg sacs with anteriorly and posteriorly directed lobes and attaching at about mid-length to the genital apertures; excessive development of the lateral processes; the presence of a lobate endopod on leg 2; and the reduction of the caudal rami which bear a spatulate seta V. However, recently described members of both genera are often not separated by this combination of characters. For instance, *S. helianthus* Uyeno and Nagasawa, 2012 and *S. imagawai* Uyeno and Nagasawa, 2012 bear the styliiform seta V on the caudal rami (Uyeno and Nagasawa, 2012). Further, *Lomanotocola nishiharai* n. sp. bears several characters (e.g., the egg sacs attached at mid-length to genital apertures with well-developed anterior and posterior lobes, Fig. 2F, G; the leg 2 bearing a lobate endopod, Fig. 3B). Despite those characters not shared with other congeners, those are shared with *Splanchnotrophus* spp. (see Hancock and Norman, 1863; Delamare Debutteville, 1950). Since the two known species of *Lomanotocola* were originally described more than a century ago and only *L. insolens* have redescribed (Delamare Debutteville, 1950), information on several characters are insufficient or absent. Hence, it is difficult to discuss the validity and decide the diagnosis of the genus based on morphological characters described in previous studies. In this study, we assigned the new species to *Lomanotocola* because of the presence of the short lateral processes on the female prosome which is concerned to the most symbolical character of the genus. However, further observations and discussion

based on new material are required to test the division of the two genera. *Lomanotocola nishiharai* n. sp. was described as third species of the genus and the fifth splanchnotrophid reported from Japanese waters (Fujita, 1895; Uyeno and Nagasawa, 2012), the other four having been described as new species in the genera (*Splanchnotrophus*, *Ceratosomicola*, and *Majimun*).

Female splanchnotrophids typically have a highly modified body and vestigial legs (Huys, 2001). In *L. nishiharai* n. sp., the major parts of the lateral processes of adult females contain the ovaries and lack muscle tissue. Hence, the mobility of splanchnotrophid females appears to be minimal. The development of lateral processes might be an adaptation to embed themselves in the narrow body space of their hosts and to provide ample space for the large ovaries and hence increase the reproductive output.

Numerous protuberances were found on the surface of the epicuticle in the female of *L. nishiharai* n. sp. Some parasitic copepods are known to have similar structures on the integumental surface of body parts that are embedded in

their respective hosts. *Gonophysema gullmarensis* Bresciani and Lützen, 1960, which is an internal parasite of tunicates, has microvillousities over 10 µm in height forming a dense layer (Bresciani, 1986). The chordeumid copepod *Ophioika* sp., and endoparasite of brittle stars, has both numerous protuberances about 20–40 nm in height and knob-like projections with microvillousities over 200 nm in height (Østergaard and Bresciani, 2000). The pennellid, *Cardiodectes shini* Uyeno, 2013, parasitic on tiny gobiids has the cephalothorax with both short and long nipple arrays which are 50 and 300 nm in height, respectively (Hirose and Uyeno, 2016). Finally, another fish parasite, *Mihbaicola sakamakii* Uyeno, 2013, has nipple arrays about 60 nm in height (Hirose and Uyeno, 2014). According to Bresciani's (1986) review of fine structures on the copepod integument, endoparasitic species with highly transformed bodies usually absorb nutrients from the host tissues via microvillousities on the body surface. The integument of *L. nishiharai* n. sp. bears somewhat longer protuberances (0.3–1.9 µm in height) which do not form a dense layer. Since the copepod has developed (and probably functional) mouth parts (Fig. 2I), it is unclear whether the integument is involved in the absorption of host nutrients. Hirose and Uyeno (2016) implied a possibility of nipple arrays to suppress anti-parasitic activities by the host hemocytes. Ballarin et al. (2015) demonstrated that cell spreading and phagocytic activities of hemocytes were suppressed on a synthetic nipple array, and hence, the protuberances on *L. nishiharai* n. sp. may have protective functions against the cellular immune system of the host.

ACKNOWLEDGMENTS

We thank Naohisa Nishihara and Satsuki Kimura (Satoumi Science Museum, Etajima City) and Shin-ichi Uye (Hiroshima University) and Hiroko Uyeno (Kagoshima Museum of Environment: Planet Earth and its Future) for their help with fieldwork off Etajima City. This study was partially supported by JSPS KAKENHI Grant Numbers JP17HO1913 and JP17K15304 to DU.

COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

The first author, DU, conducted field surveys, observed morphological characters of the new species for taxonomic study, and prepared the manuscript. EH made histological and ultrastructural observations and revised the manuscript.

REFERENCES

- Abad M, Díaz-Agras G, Urgorri V (2011) Anatomical description and biology of the splanchnotrophid *Splanchnotrophus gracilis* Hancock & Norman, 1863 found parasitizing the doridacean nudibranch *Trapania tartanella* Ihering, 1886 at the Ria de Ferrol (Galicia, NW Iberian Peninsula). *Thalassas* 27(2): 49–60
- Anton RF, Schrödl M (2013) The gastropod-crustacean connection: towards the phylogeny and evolution of the parasitic copepod family Splanchnotrophidae. *Zool J Linn Soc* 167: 501–530
- Anton RF, Schories D, Jörgen KM, Kaligis F, Schrödl M (2016) Description of four new endoparasitic species of the family Splanchnotrophidae (Copepoda, Poecilostomatoida) from nudibranch and sacoglossan gastropod hosts. *Mar Biodivers* 46: 183–195
- Ballarin L, Franchi N, Gasparini F, Caicci F, Miyauchi A, Hirose E (2015) Suppression of cell-spreading and phagocytic activity on nano-pillared surface: in vitro experiment using hemocytes

- of the colonial ascidian *Botryllus schlosseri*. *Invert Surviv J* 12: 82–8
- Boxshall GA, Halsey SH (2004) *An Introduction to Copepod Diversity*. Ray Society, London
- Bresciani J (1986) The fine structure of the integument of free-living and parasitic copepods. A review. *Acta Zool* 67: 125–145
- Delamare Deboutteville C (1950) Contribution à la connaissance des Copépodes du genre *Splanchnotrophus* Hancock et Norman parasites de Mollusques. *Vie Milieu* 1: 74–80
- Fujita T (1895) On the parasitic Copepoda. *Dobutsugaku Zasshi [Zoological Magazine]* 7: 57–60
- Hancock A, Norman AM (1863) On *Splanchnotrophus*, an undescribed genus of Crustacea, parasitic on nudibranchiate Mollusca. *Trans Linn Soc Lond, Zool* 24: 49–60
- Haumayr U, Schrödl M (2003) Revision of the endoparasitic copepod genus *Ismaila* Bergh, 1867, with description of eight new species (Copepoda, Poecilostomatoida, Splanchnotrophidae). *Spixiana* 26: 1–33
- Hecht E (1895) Contribution à l'étude des Nudibranches. *Mémoires de la Société Zoologique de France* 8: 539–711, pls. 1–5
- Hirose E, Uyeno D (2014) Histopathology of a mesoparasitic hatschekiid copepod in hospite: Does *Mihbaicola sakamakii* (Copepoda: Siphonostomatoida: Hatschekiidae) fast within the host fish tissue? *Zool Sci* 31: 546–552
- Hirose E, Uyeno D (2016) Regional differentiation of the cuticular surface structure in the mesoparasitic copepod *Cardiodectes shini* (Siphonostomatoida: Pennellidae) on a pygmy goby. *Invert Surviv J* 13: 134–139
- Humes AG, Gooding RU (1964) A method for studying the external anatomy of copepods. *Crustaceana* 6: 238–240
- Huys R (2001) Splanchnotrophid systematics: a case of polyphyly and taxonomic myopia. *J crust Biol* 21: 106–156
- Marshall HG, Hayward PJ (2006) The effects of *Splanchnotrophus willemi* infecting *Ancula gibbosa* (Gastropoda: Opisthobranchia: Nudibranchia). *J mar biol Assoc UK* 86: 1437–1441
- Monod T, Dollfus RP (1932) Les Copépodes parasites de mollusques. *Ann Parasitol Hum Comp* 10: 129–204
- Norman AM, Scott T (1906) *The Crustacea of Devon and Cornwall*. W. Wesley and Son, London
- Østergaard P, Bresciani J (2000) SEM and TEM study of the integument of *Ophioika* sp. (Crustacea, Copepoda). *J crust Biol* 20: 674–679
- Salmen A, Kaligis F, Mamangkey GE, Schrödl M (2008a) *Arthurius bunakenensis*, a new tropical Indo-Pacific species of endoparasitic copepods from a sacoglossan opisthobranch host (Crustacea, Copepoda, Poecilostomatoida, Splanchnotrophidae). *Spixiana* 31: 199–205
- Salmen A, Wilson NG, Schrödl M (2008b) Scanning electron microscopical description and biology of three new endoparasitic *Ceratosomicola* species from tropical Indo-Pacific nudibranch hosts (Crustacea, Copepoda, Poecilostomatoida, Splanchnotrophidae). *Spixiana* 31: 47–69
- Schrödl M (2002) Heavy infestation by endoparasitic copepod crustaceans (Poecilostomatoida: Splanchnotrophidae) in Chilean opisthobranch gastropods, with aspects of splanchnotrophid evolution. *Org Div Evol* 2: 19–26
- Scott T, Scott A (1895) On some new and rare British Copepoda. *Ann Mag Nat Hist* (6) 16: 353–362
- Uyeno D, Nagasawa K (2012) Four new species of splanchnotrophid copepods (Poecilostomatoida) parasitic on doridacean nudibranchs (Gastropoda, Opisthobranchia) from Japan, with proposition of one new genus. *ZooKeys* 247: 1–29
- Wolf M, Young CM (2014) Impacts of an endoparasitic copepod, *Ismaila belciki*, on the reproduction, growth and survivorship of its nudibranch host, *Janolus fuscus*. *Int J Parasitol* 44: 391–401

(Received January 15, 2018 / Accepted March 25, 2018)