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Systematic revision of the pennellid genus *Creopelates* Shiino, 1958 (Copepoda: Siphonostomatoida) and the proposal of a new genus

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Abstract

The parasitic copepod *Creopelates floridus* Shiino, 1958 (Siphonostomatoida: Pennellidae) is redescribed based on post-metamorphic adult females in the collection of the Imperial Majesty of Japan deposited in the National Museum of Nature and Science, Tsukuba (NSMT), Japan. Five new species of pennellid copepods are described based on postmetamorphic adult females from marine actinopterygian fishes newly collected in littoral waters of Japan and the Philippines, in the western North Pacific. The copepods and their hosts are as follows: *Creopelates hosinoi* **n. sp.** from *Bryaninops yongei* (Davis & Cohen) (Perciformes: Gobiidae); *C. shirakawai* **n. sp.** from *Diancistrus fuscus* (Fowler) (Ophidiiformes: Bythitidae); *C. lubangensis* **n. sp.** from *Gobiodon rivulatus* (Rüppell) (Perciformes: Gobiidae); *Nagasawanus akino-hama* **n. gen. et n. sp.** from *Trimma grammistes* (Tomiya) (Perciformes: Gobiidae); *N. snufkini* **n. gen. et n. sp.** from *T. tevegae* Cohen & Davis. The total number of valid species contained in the genus *Creopelates* is now five. *Nagasawanus* **n. gen.** is distinguishable from other pennellid genera by the following features: antennary processes and cephalic lobes rounded without branched fringes, neck region without processes, maxilla with claw-like terminal segment lacking spinules. Keys to the genera of Pennellidae and to the species of *Creopelates* and *Nagasawanus* **n. gen.** are also provided.

Key words: parasitic copepods, pennellid, mesoparasite, goby, SCUBA diving

Introduction

The Pennellidae Burmeister, 1835 (Copepoda: Siphonostomatoida) is one of the major families of parasitic copepods on marine fishes. The family contains about 140 species 22 genera (e.g., Boxshall & Halsey, 2004; Boxshall & Walter 2014; Castro-Romero, 2014), most of which are mesoparasites (Kabata 1979; Boxshall & Halsey 2004). Several species, e.g., *Lernaocera branchialis* (Linnaeus, 1767), are known to infest commercially important fishes, and they have been well studied (e.g., Kabata 1970, 1981, 1984). On the other hand, pennellid copepods have been also described from non-commercial fishes, e.g., small coastal fishes and deep-sea fishes (e.g., Shiino 1956, 1958; Izawa 1970, 1977; Kabata 1972; Blasiola 1979; Boxshall 1986). Very few faunal studies of the pennellids of non-commercial fishes have been undertaken so the species richness of this family is poorly known. As a result of recent surveys in Japanese waters, seven new species of pennellids have been described from small coastal fishes (Uyeno & Nagasawa 2010a, b; Uyeno 2013).

The pennellid genus *Creopelates* Shiino, 1958 which currently includes two species is a mesoparasite of marine actinopterygian fishes (Shiino 1958; Uyeno & Nagasawa 2010b). Shiino (1958) described *C. floridus* Shiino, 1958 from *Zalanthias kelloggi* (Jordan & Evermann) (= *Z. azumanus*) (Perciformes: Serranidae) based on postmetamorphic adult females collected from Sagami Bay, North Pacific Ocean, Japan, and he established *Creopelates* based on this species. However, some appendages of the copepod were not described in the original description. A second species, *C. nohmijimensis* Uyeno & Nagasawa, 2010, was described based on postmetamorphic adult females from *Priolepis borea* (Snyder) (Perciformes: Gobiidae) caught in the Seto Inland Sea, Japan.

In this paper, *C. floridus* is redescribed based on the type series and the diagnosis of *Creopelates* is redefined. Five new species of pennellids are described based on newly collected specimens in littoral waters of Japan and the Philippines. Additionally, a new pennellid genus, *Nagasawanus* **n. gen.**, is established.

Material and methods

Freshly caught marine fishes for this study were collected while SCUBA diving in the western North Pacific. The parasitic copepods were carefully removed from the hosts under a dissecting microscope and preserved in 99% ethanol. Copepods were subsequently soaked in lactophenol for 12 h, dissected, and examined following the procedure of the wooden slide (Humes & Gooding 1964). 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 as the range followed by the mean and standard deviation in parentheses. Body length was measured from the rostrum to abdomen. Type specimens are deposited in the crustacean collection of the National Museum of Nature and Science, Tsukuba (NSMT), Japan, the University of the Ryukyus Museum, Fujukan (RUMF), Japan, the National Museum of the Philippines (NMP) and the Florida Museum of Natural History (FLMNH), Florida, U.S.A.

Results

Order Siphonostomatoida Burmeister, 1835

Family Pennellidae Burmeister, 1835

Genus *Creopelates* Shiino, 1958

Creopelates: Shiino, 1958, p. 92

Diagnosis of postmetamorphic adult female. Body long, comprising cephalothorax, elongate neck region and trunk; junction of neck and trunk curved. Cephalothorax bearing paired globular antennary processes and paired posterolateral lobes; rostrum convex. Neck region narrow, fringed with finely digitate lobes arranged in more than one pair. Trunk pyriform, longer than wide, with anterior end narrowing towards neck region. Abdomen conical, without brush-like processes; located between oviducal pores. Egg-sac uniseriate, coiled or in single plane.

Antennule unsegmented, bearing about 28 setae and one distal aesthetasc; 2 of distal setae sharing common base. Antenna 3-segmented, chelate, typical pennellid shaped; proximal segment unarmed or bearing distal projection; middle segment bearing pointed protrusions along inner medial margin, terminal segment claw-like with small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule bilobate; lobes bearing one or two elements on tip. Maxilla 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment incompletely subdivided bearing tip covered with small spinules. Maxilliped absent.

Legs 1 and 2 biramous, situated on posterior part of cephalothorax and second pediger. Legs 3 and 4 uniramous, situated on third pediger and distal part of neck, respectively. Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	1/0–0	0–0; 5	Absent

Adult male. Unknown.

Type species. *Creopelates floridus* Shiino, 1958

Remarks. *Creopelates* is clearly distinguishable from other pennellid genera by the general body shape of postmetamorphic female which comprises the cephalothorax with paired globular antennary processes and paired posterolateral lobes, the elongate neck region with at least one pair of lobes with digitate fringes, and the pyriform trunk bearing abdomen without brush-like processes.

Creopelates floridus Shiino, 1958

Japanese name: Uo-no-wakizashi for both the genus and the species
(Figs 1A, 2–3)

Creopelates floridus: Shiino, 1958, p. 92–96

Type material. Holotype: postmetamorphic adult female (NSMT-Cr R 1225a) (dissected), ex *Plectranthias sagamiensis* (Katayama) (Perciformes: Serranidae), Kannonzुकadashi, Amadaiba, Hayama, Sagami Bay, Kanagawa, North Pacific Ocean, Japan, 65 m depth, 17 January, 1957. Paratypes: 2 postmetamorphic adult females (NSMT-Cr R 1225b) (dissected), collection data same as those of holotype.

Additional material. 1 postmetamorphic adult female (NSMT-Cr R 1686), ex *P. sagamiensis*, Kannonzuka, Amadaiba, Hayama, Sagami Bay, North Pacific Ocean, Japan, 75 m depth, 20 January, 1960; 2 postmetamorphic adult females (NSMT-Cr R 1260), ex *P. sagamiensis*, Kannonzuka-dashi, Amadaiba, Hayama, Sagami Bay, North Pacific Ocean, Japan, 62–72 m depth, 13 March, 1957.

Redescription of holotype and paratype female. Body (Fig. 2A) 11.56–14.68 (13.31 ± 1.60) long ($n = 3$), comprising cephalothorax, neck region and trunk; junction of neck and trunk curved. Cephalothorax (Fig. 2A–C) wider than long 0.79–1.09 (0.93 ± 0.15) \times 1.17–1.43 (1.27 ± 0.14), bearing paired antennary processes with multiple, irregular accessory processes, and paired posterolateral lobes expanded posteriorly with digitate processes; rostrum (Fig. 2D) convex with blunt tip. Neck region (Fig. 2A) narrow, bearing paired small digitate lobes anteriorly (Fig. 2A–C) and fringed with series of finely digitate lobes, arranged in about ten pairs (Fig. 2A); second and third pedigers clearly segmented. Trunk (Fig. 2A, E) pyriform, longer than wide 3.90–4.45 (4.25 ± 0.31) \times 1.54–2.17 (1.77 ± 0.35), with anterior end narrowing towards neck region, with slightly protruding posterolateral corners (Fig. 2E). Abdomen located between paired oviducal pores (Fig. 2A, E, F). Egg-sacs uniseriate, spirally coiled, or single plane (Fig. 2A).

Antennule (Fig. 2G) unsegmented, bearing 19 setae along anterior margin: distal tip with 9 setae distally, 2 of which share common base, and 1 aesthetasc. Antenna (Fig. 3A) 3-segmented, chelate, typical pennellid; proximal segment bearing distal pointed process on posterior surface; middle segment bearing two pointed protrusions along inner medial margin, terminal segment claw like with small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 3B) comprising element with flanged distal part and one accessory seta and lobe with two distal setae. Maxilla (Fig. 3C) 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment incompletely 2-segmented, with rounded distal part bearing spatulate fringe covered with small spinules. Maxilliped absent.

Legs 1 and 2 (Fig. 3D, E) biramous, situated on posterior part of cephalothorax to second pediger (Fig. 2C). Legs 3 and 4 (Fig. 3F–H) uniramous, situated on third pediger and distal part of neck, respectively. Legs 4 separated by gap from preceding legs. Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	1–0	0–0; 5	Absent

Protopods of legs 3 and 4 separated from respective intercoxal sclerites by long gaps (Fig. 3F, G).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk behind the base of the pectoral fin and attached to the host's vertebrae, while its trunk and egg sacs remained outside the fish's body wall (Fig. 1A).

Variability. The morphology of the non-type material is as in the type series. The measurements of the paratype ($n = 1$) are as follows: body length 13.51 mm; cephalothorax length 0.96; trunk length 4.41; trunk width 1.31.

Remarks. This copepod is the type species of the genus *Creopelates*. *Creopelates floridus* Shiino, 1958 was described based on three females obtained from *Zalanthias kelloggi* (Jordan & Evermann) (= *Z. azumanus*) (Perciformes: Serranidae) collected in Sagami Bay, Japan (Shiino 1958). However, from the re-examination of the type host specimens of the types deposited together with the copepods in NSMT, it was revealed that they are actually *Plectranthias sagamiensis* (Katayama) (Perciformes: Serranidae).

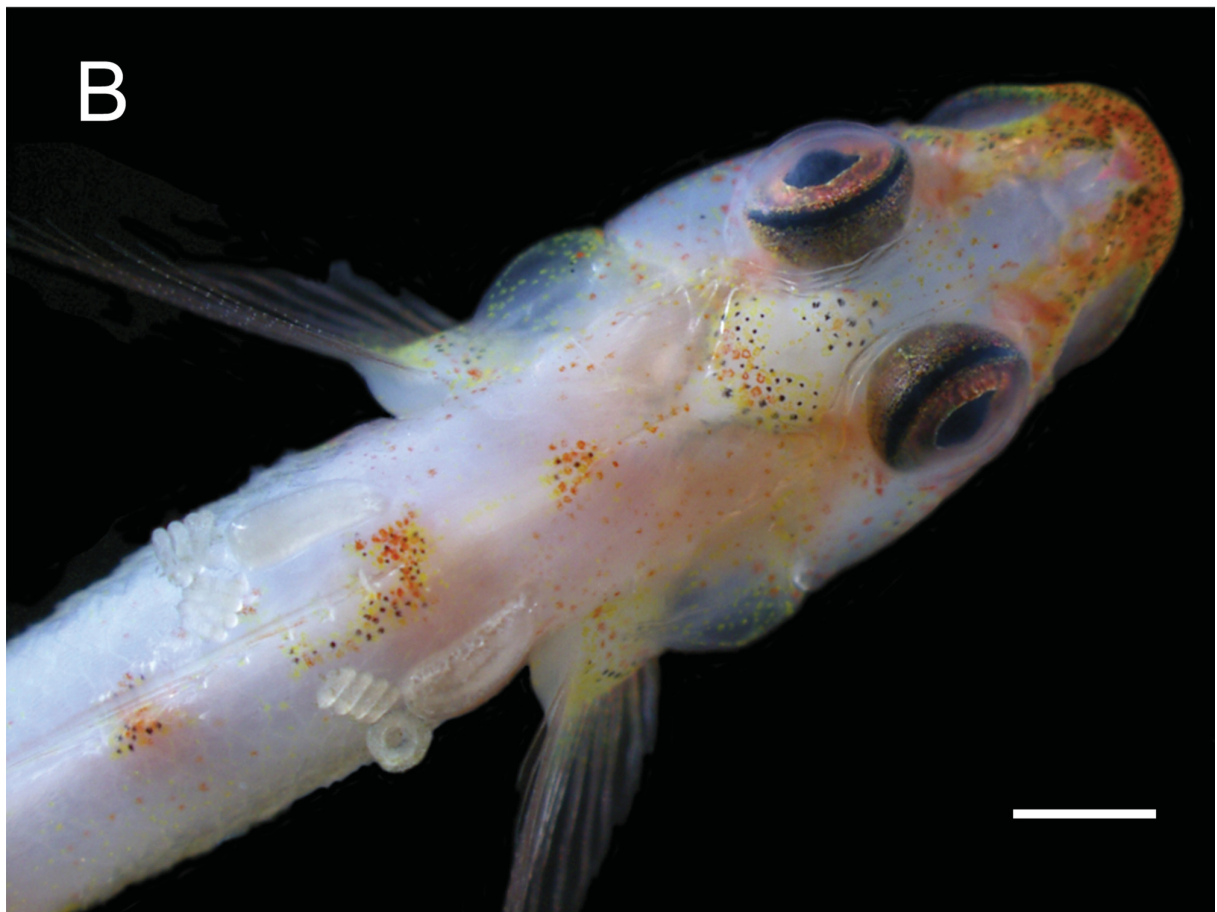


FIGURE 1. Postmetamorphic adult females of *Creopelates floridus* Shiino, 1958 (A) and *C. hoshinoi* n. sp. (B) attached to their hosts. A, a specimen of *Plectranthias sagamiensis* (Katayama) infected by a non-type female, NSMT-Cr R 1260, of *C. floridus*; B, two specimens of *C. hoshinoi* n. sp. attached to the host, *Bryaninops yongei* (Davis & Cohen). Scale bars: A, 10 mm; B, 2 mm.

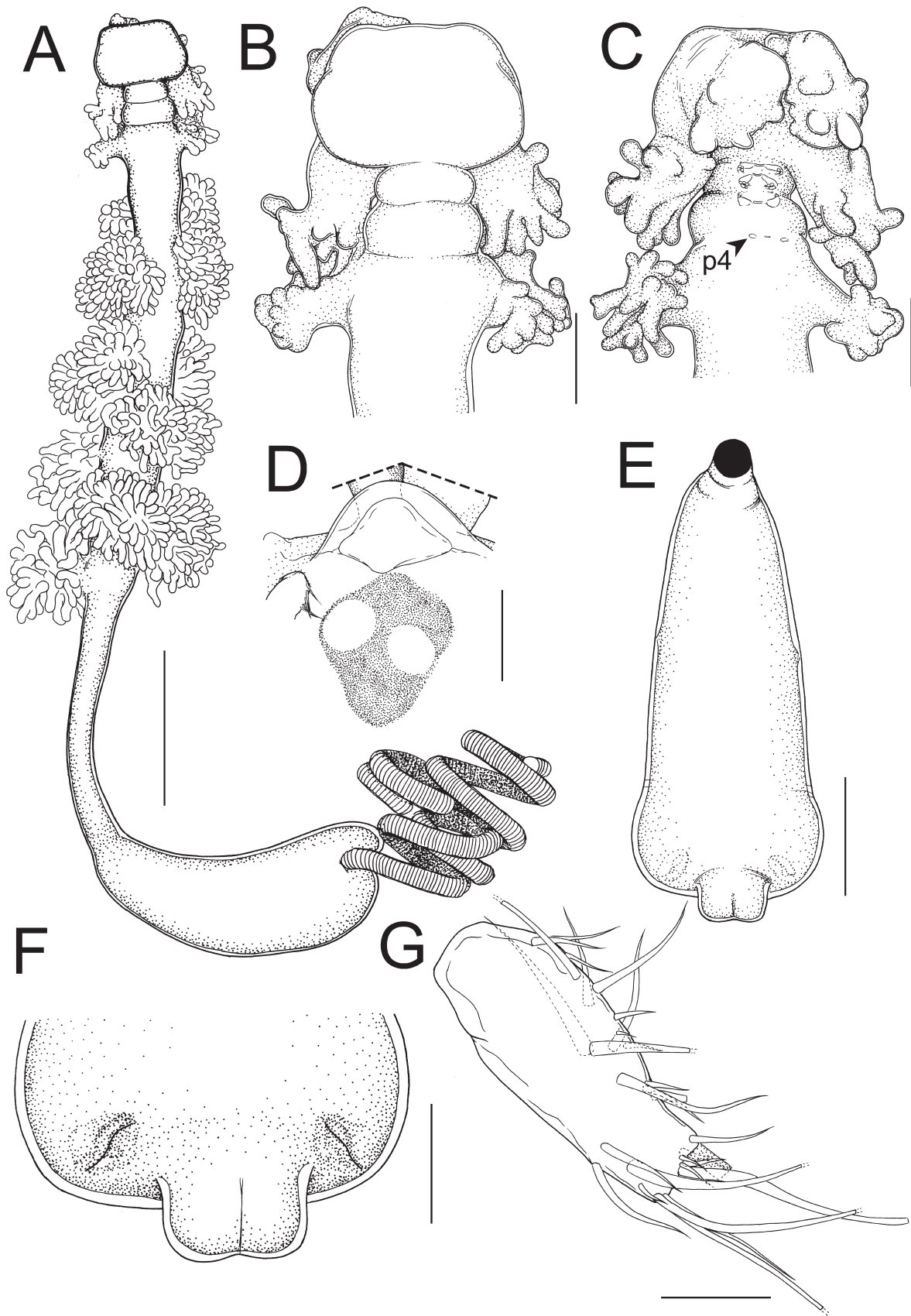


FIGURE 2. *Creopelates floridus* Shiino, 1958, postmetamorphic adult female, paratype NSMT-Cr R 1225b. A, habitus; B, cephalothorax and anterior end of neck region, dorsal; C, same, ventral, p4 = leg 4; D, anterior part of cephalothorax with rostrum; E, trunk, ventral; F, posterior part of trunk with abdomen, ventral; G, right antennule, anterior. Scale bars: A, 2000 μ m; B, C, 500 μ m; D, 50 μ m; E, 1000 μ m; F, 200 μ m; G, 20 μ m.

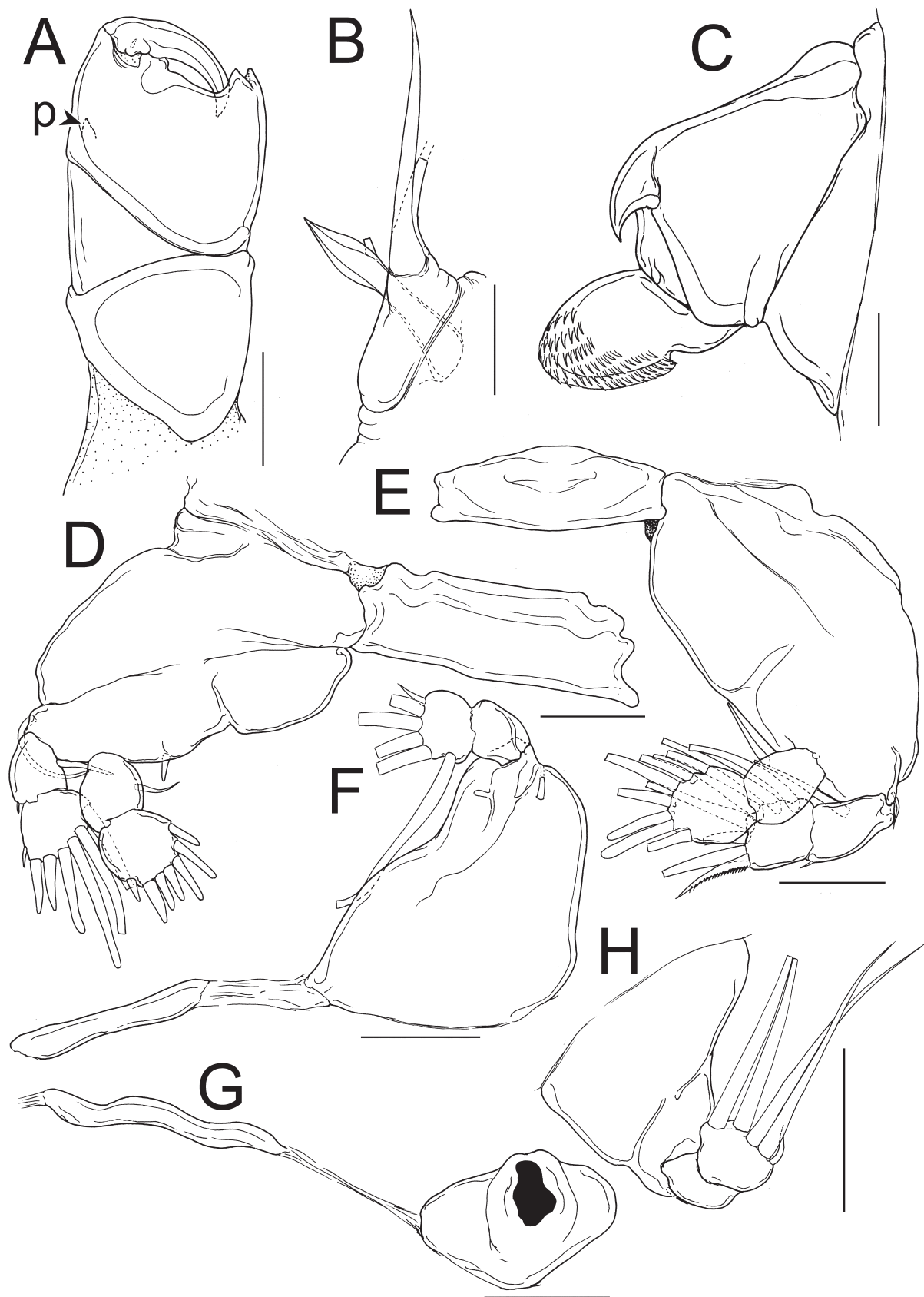


FIGURE 3. *Creopelates floridus* Shiino, 1958, postmetamorphic adult female, paratype NSMT-Cr R 1225b. A, left antenna, anterior, p = process on proximal segment; B, left maxillule, anterior; C, left maxilla, anterior; D, left leg 1 with intercoxal sclerite, anterior; E, right leg 2 with intercoxal sclerite, anterior; F, left leg 3 with intercoxal sclerite, posterior; G, left leg 4 with intercoxal sclerite, posterior; H, left leg 4, posterior. Scale bars: A–C, 20 μ m; D–H, 30 μ m.

Creopelates nohmijimensis Uyeno & Nagasawa, 2010

Japanese name: Haze-no-wakizashi

Creopelates nohmijimensis: Uyeno & Nagasawa, 2010, p. 30–33

Type material. Holotype: female (NSMT–Cr 21191) (dissected), ex *Priolepis borea* (Snyder) (Perciformes: Gobiidae), off Irukabana (34°13'N, 132°23'E), Nohmijima Island, Hiroshima, Seto Inland Sea, Japan, 15 m depth, 12 September 2009, leg. D. Uyeno. Paratypes: 2 females (NSMT–Cr 21192), ex *P. boreus* off Irukabana, Nohmijima Island, Hiroshima, Seto Inland Sea, Japan, 15 m depth, 12 September 2009, leg. D. Uyeno.

Remarks. Described by Uyeno & Nagasawa (2010b) based on three postmetamorphic adult females in the Seto Inland Sea. See original description.

Creopelates hoshinoi n. sp.

New Japanese name: Hoshino-no-wakizashi

(Figs 1B, 4, 5)

Type material. Holotype: postmetamorphic adult female (NSMT–Cr 23841) (dissected), ex *Bryaninops yongei* (Davis & Cohen) (Perciformes: Gobiidae), off Akinohama (34°47'N, 139°23'E), Izu-Oshima Island, Tokyo, North Pacific Ocean, Japan, 20 m depth, 6 January 2011, leg. O. Hoshino. Paratype: 1 postmetamorphic adult female (NSMT–Cr 23842), ex *Bryaninops yongei* (Davis & Cohen) (Perciformes: Gobiidae), off Akinohama (34°47'N, 139°23'E), Izu-Oshima Island, Tokyo, North Pacific Ocean, Japan, 30 m depth, 11 January 2012, leg. O. Hoshino.

Description of postmetamorphic adult female. Body (Fig. 4A) 4.67 long, comprising cephalothorax, neck region and trunk; junction of neck and trunk curved. Cephalothorax (Fig. 4A–C) longer than wide 0.48×0.32 , bearing paired antennary processes with irregular processes and paired small posterolateral lobes; rostrum (Fig. 4D) flat, bearing straight frontal margin. Neck region (Fig. 4A) narrow, fringed with one pair of finely digitate lobes (Fig. 4A–C). Trunk (Fig. 4A, E) pyriform, longer than wide 2.44×0.88 , with anterior end narrowing towards neck region (Fig. 4E). Abdomen located between oviducal pores (Fig. 4A, E, F). Egg-sac uniseriate, spirally coiled (Fig. 4A).

Antennule (Fig. 4G) unsegmented, bearing at least 14 setae along anterior margin: distal tip with 10 setae distally, 2 of which share common base, and 1 aesthetasc. Antenna (Fig. 5A) 3-segmented, chelate, typical pennellid; proximal segment bearing pointed outer process; middle segment bearing one pointed protrusion serrated along inner medial margin; terminal segment claw-like with minute element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 5B) comprising one seta and lobe with two distal setae. Maxilla (Fig. 5C) 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment incompletely subdivided, with rounded distal part covered with small spinules. Maxilliped absent.

Legs 1 and 2 (Fig. 5D, E) biramous. Legs 3 and 4 (Fig. 5F, G) uniramous. Legs 1 to 4 evenly arrayed on posterior part of cephalothorax to neck region (Fig. 4C). Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	0–0	0–0; 5	Absent

Protopods of legs 1–4 connected to respective intercoxal sclerites (Fig. 5D–G).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk dorsally behind the base of the pectoral fin, while its trunk and egg sacs remained external to the fish's body wall (Fig. 1B).

Variability of female morphology. The morphology of the female paratype is as in the holotype. The measurements of the paratype are as follows ($n = 1$): body length 4.10; cephalothorax length 0.34; cephalothorax width 0.24; trunk length 1.95; trunk width 0.63.

Remarks. *Creopelates hoshinoi* n. sp. differs from *C. floridus* and *C. nohmijimensis* in having cephalic lobes without fringed digitate fringes (vs. with digitate fringes in the latter species) and the neck region is fringed with one pair of finely digitate lobes (vs. about ten pairs of lobes).

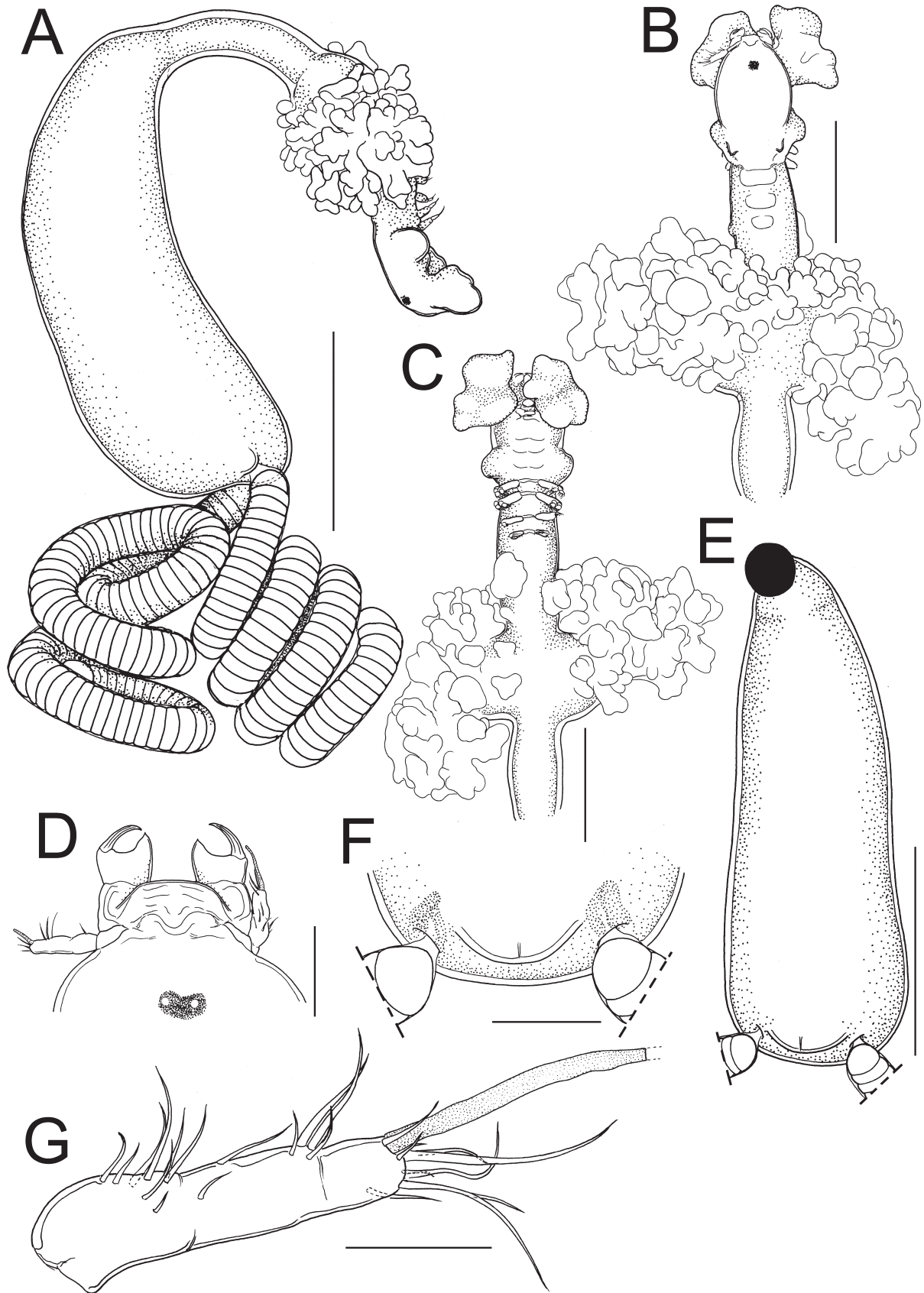


FIGURE 4. *Creopelates hoshinoi* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23841. A, habitus; B, cephalothorax and neck region, dorsal; C, same, ventral; D, anterior part of cephalothorax with rostrum; E, trunk, ventral; F, posterior part of trunk, ventral; G, right antennule, anterior. Scale bars: A, E, 1000 μ m; B, C, 500 μ m; D, 100 μ m; F, 300 μ m; G, 30 μ m.

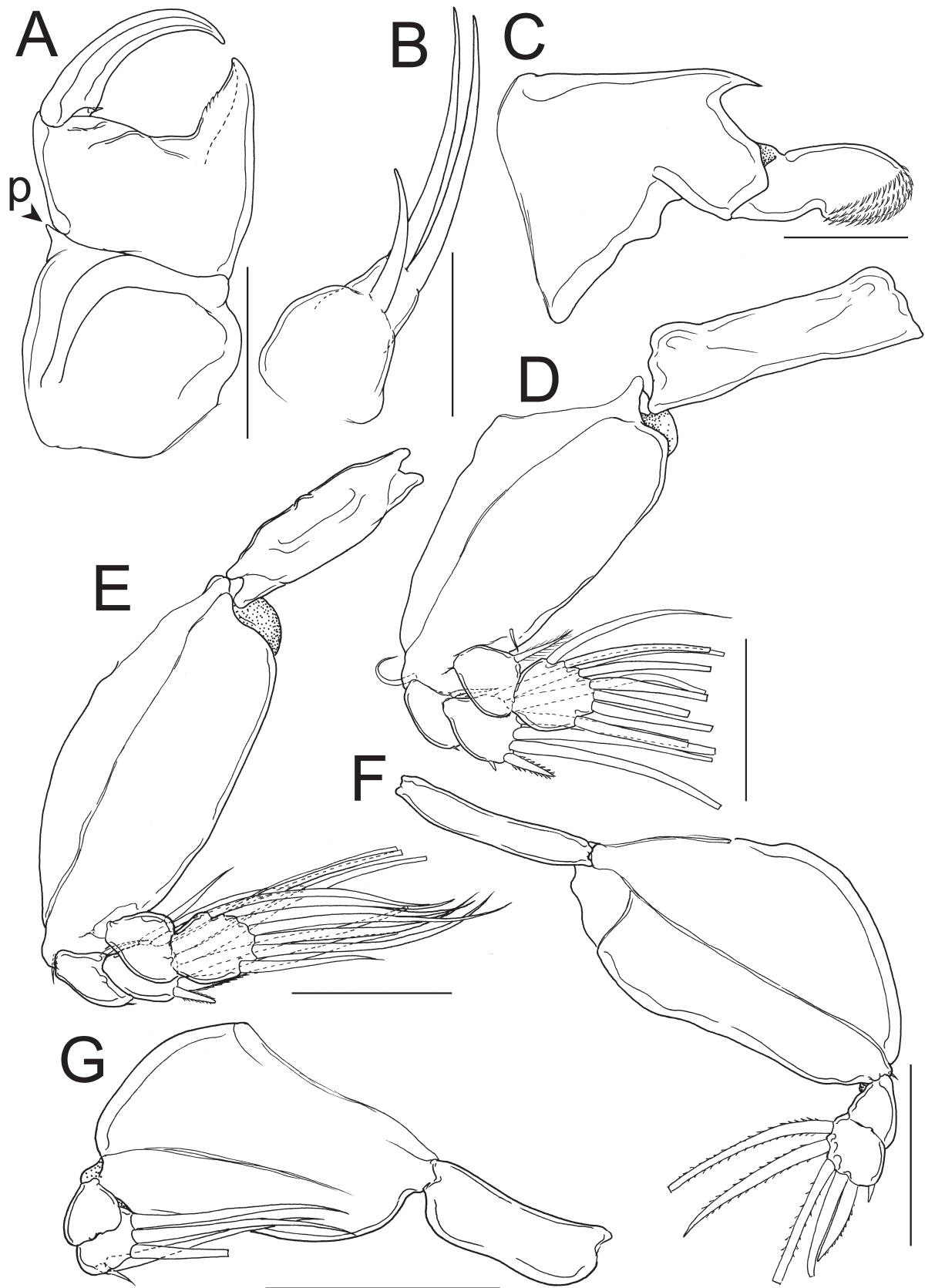


FIGURE 5. *Creopelates hoshinoi* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23841. A, left antenna, anterior, p = process on proximal segment; B, left, maxillule; C, right maxilla, anterior; D, right leg 1 with intercoxal sclerite, anterior; E, right leg 2 with intercoxal sclerite, anterior; F, left leg 3 with intercoxal sclerite, anterior; G, right leg 4 with intercoxal sclerite, anterior. Scale bars: A, D–G, 50 µm; B, C, 30 µm.

Etymology. The specific name of the new species, *hoshinoi*, is dedicated to Mr. Osamu Hoshino, an outstanding professional diver working at Izu Oshima Island, who collected the type material.

***Creopelates shirakawai* n. sp.**

New Japanese name: Shirakawa-no-wakizashi
(Figs 6A, B, 7, 8)

Type material. Holotype: postmetamorphic adult female (NSMT-Cr 23843) (dissected), ex *Diancistrus fuscus* (Fowler) (Ophidiiformes: Bythitidae), off Awa (26°36'N, 127°55'E), Nago Bay, Okinawa Island, Japan, 5 m depth, 8 December, 2011, leg. N. Shirakawa.

Description of postmetamorphic adult female. Body (Fig. 7A) 7.55 long, comprising cephalothorax, neck region and trunk; junction of neck and trunk curved. Cephalothorax (Fig. 7A–C) round, 1.09 × 1.08, with paired vertically long antennary processes with rugged surface and paired posterolateral lobes with digitate fringes; rostrum (Fig. 7D) not well developed, bearing straight frontal margin. Neck region (Fig. 7A) narrow, fringed with series of less than ten pairs of finely digitate lobes; second and third pedigers clearly segmented (Fig. 7B, C). Trunk (Fig. 7A, E) pyriform, longer than wide 2.76 × 1.06, with anterior end narrowing towards neck region (Fig. 7E). Abdomen conical, bearing median depression, located between oviducal pores (Fig. 7A, E, F). Egg-sac uniseriate, coiled (Fig. 7A).

Antennule (Fig. 7G) unsegmented, bearing 18 setae along anterior margin: distal tip with 11 setae distally, 2 of which share common base, and 1 aesthetasc. Antenna (Fig. 8A) 3-segmented, chelate, typical pennellid; proximal segment bearing blunt distal process on outer margin; middle segment bearing two small pointed protrusions along inner medial margin; terminal segment claw-like bearing small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 8B) comprising one seta and lobe with two distal setae. Maxilla (Fig. 8C) 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment incompletely subdivided, with rounded distal part bearing spatulate fringe covered with small spinules. Maxilliped absent.

Legs 1 and 2 (Fig. 8D–G) biramous. Legs 3 and 4 (Fig. 8H, I) uniramous. Legs 1–4 evenly arrayed on posterior part of cephalothorax to neck region (Fig. 7C). Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	0–0	0–0; 5	Absent

Protopods of legs 1–4 connected to respective intercoxal sclerites (Fig. 8E, G, H, I).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk near the anus and attached to the vertebrae, while its trunk and egg sacs remained external to the fish's body wall (Fig. 6A, B).

Remarks. *Creopelates shirakawai* n. sp. differs from *C. floridus*, *C. nohmijimensis* and *C. hoshinoi* n. sp. in having antennary processes without digitate fringes and cephalic lobes with digitate fringes.

Etymology. The specific name “*shirakawai*” is dedicated to Mr. Naoki Shirakawa, an expert diver who finds remarkable animals. He collected the type specimen of this copepod.

***Creopelates lubangensis* n. sp.**

(Figs 6C, D, 9, 10)

Type material. Holotype: postmetamorphic adult female (NMCR 39115) (dissected), ex *Gobiodon rivulatus* (Rüppell) (Perciformes: Gobiidae), off Pangpang (13°48'N, 120°5'E), Lubang Island, Mindro, South China Sea, Philippines, 5 m depth, 23 May, 2014, leg. A. Ackiss, M. Lane, and D. Uyeno. Paratype: 1 postmetamorphic adult female (UF 40383), collection data same as those of holotype.

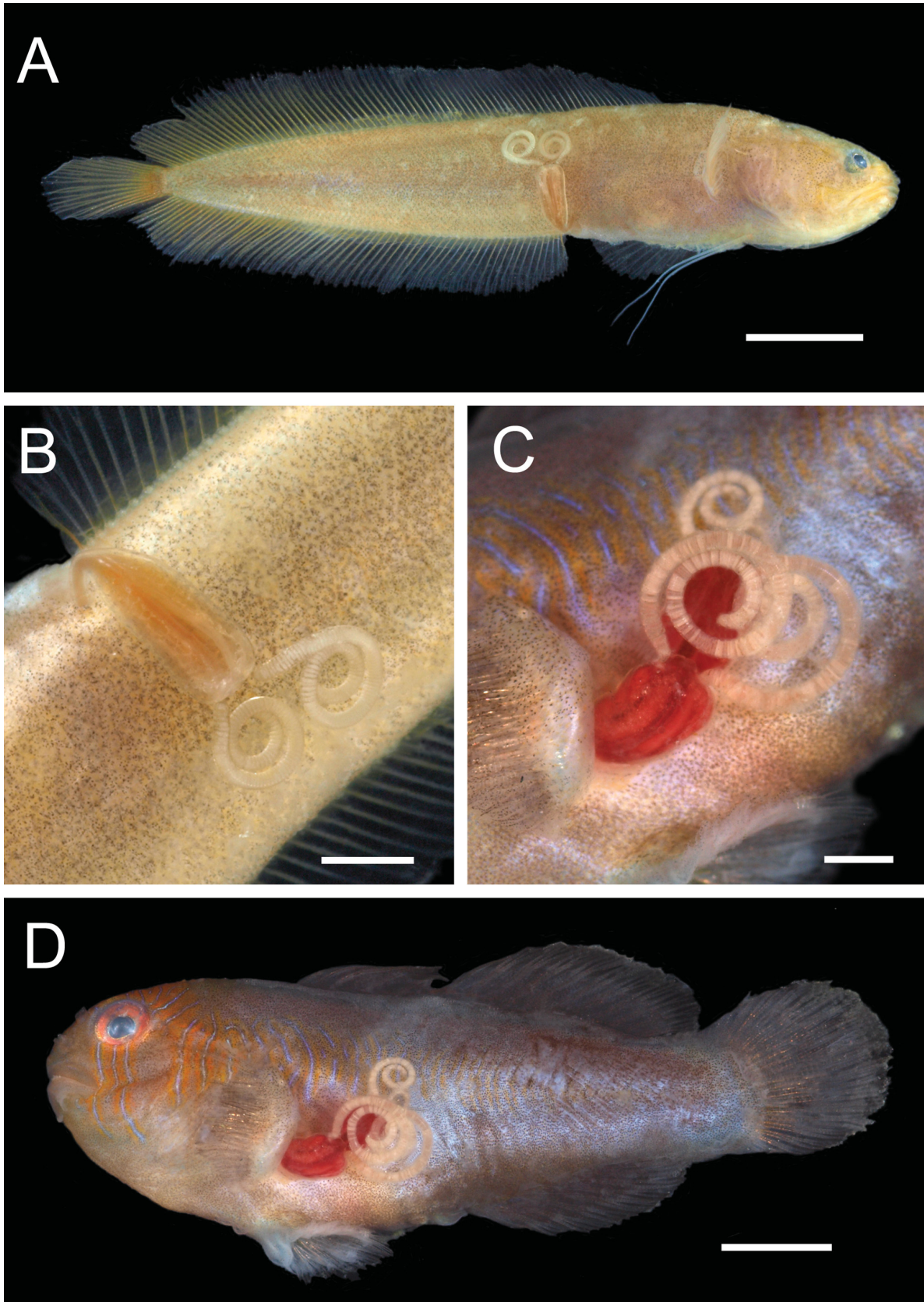


FIGURE 6. Postmetamorphic adult females of *Creopelates shirakawai* n. sp. (A, B) and *C. lubangensis* n. sp. (C, D) attached to their hosts. A, a specimen of *Diacistrus fuscus* (Fowler) infected by the holotype female, NSMT-Cr 23843; B, coloration in life of holotype attached to host's body; C, coloration in life of type series, NMCR 39115 and UF 40383, attached to host's body; D, a specimen of *Gobiodon rivulatus* (Rüppell) infected by the holotype and the paratype females. Scale bars: A, 5 mm; B, 2 mm; C, 1 mm; D, 3 mm.

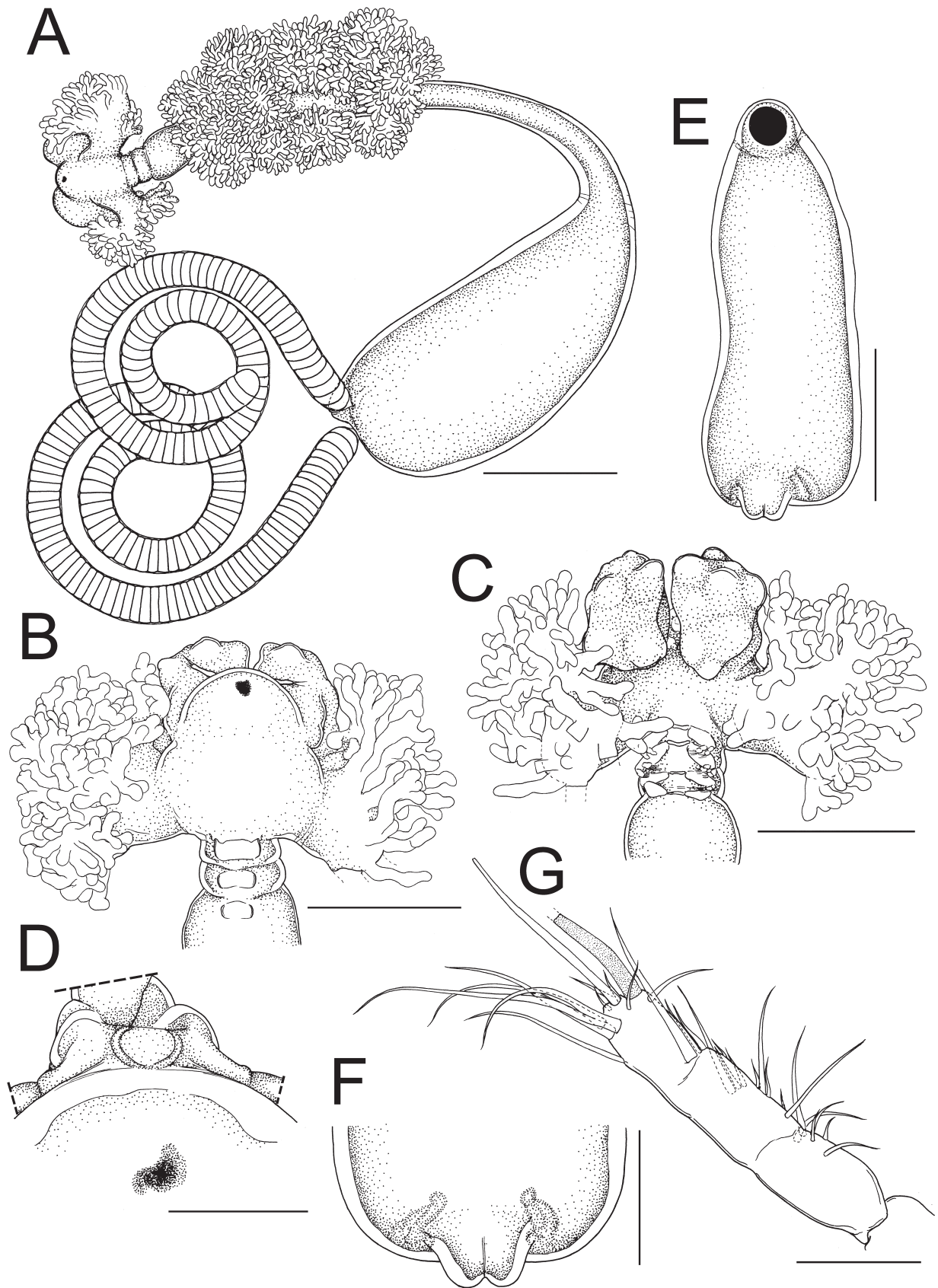


FIGURE 7. *Creopelates shirakawai* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23843. A, habitus; B, cephalothorax and anterior end of neck region, dorsal; C, same, ventral; D, anterior part of cephalothorax with rostrum; E, trunk, ventral; F, posterior part of trunk, ventral; G, left antennule, anterior. Scale bars: A, E, 1000 μ m; B, C, F, 500 μ m; D, 100 μ m; G, 30 μ m.

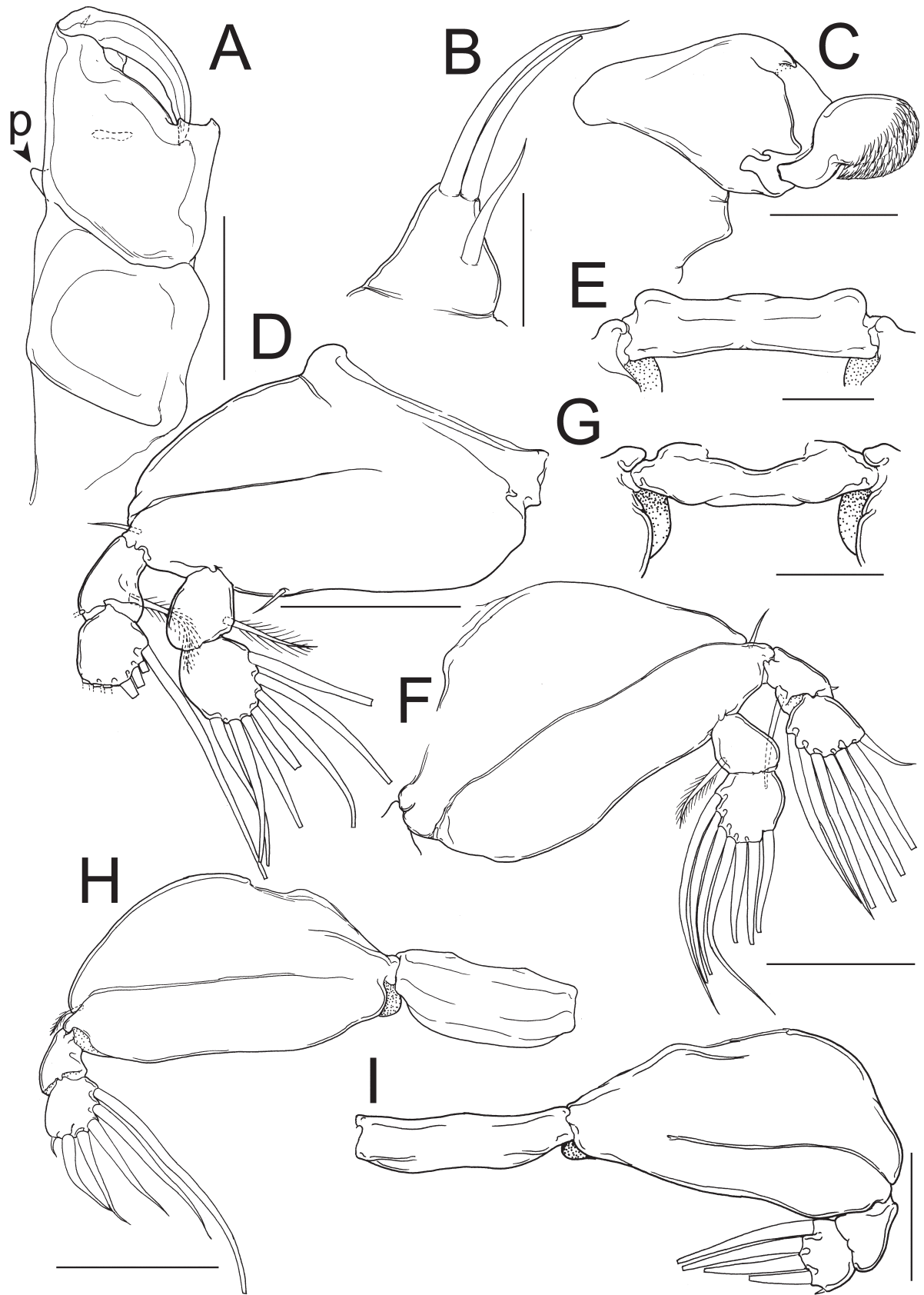


FIGURE 8. *Creopelates shirakawai* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23843. A, left antenna, anterior, p = process on proximal segment; B, right maxillule; C, right maxilla, anterior; D, right leg 1, anterior; E, intercoxal sclerite of leg 1; F, left leg 2, anterior; G, intercoxal sclerite of leg 2; H, right leg 3 with intercoxal sclerite, anterior; I, left leg 4 with intercoxal sclerite, anterior. Scale bars: A, D, F, H, 50 μ m; B, C, E, G, I, 30 μ m.

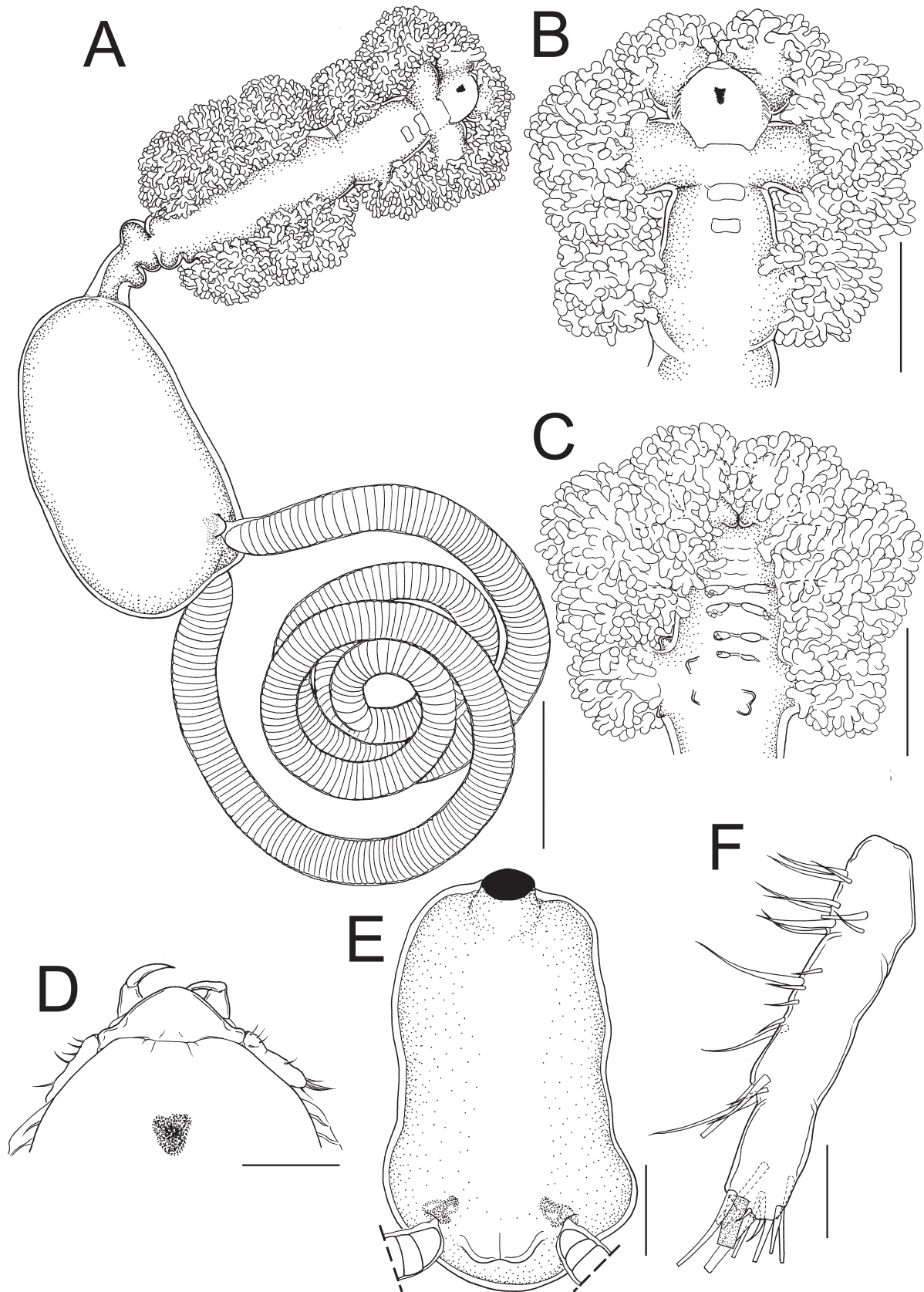


FIGURE 9. *Creopelates lubangensis* n. sp., postmetamorphic adult female, holotype, NMCR 39115. A, habitus; B, cephalothorax and anterior end of neck region, dorsal; C, same, ventral; D, anterior part of cephalothorax with rostrum; E, trunk, ventral; F, left antennule, anterior. Scale bars: A, 1000 μ m; B, C, E, 500 μ m; D, 100 μ m; F, 20 μ m.

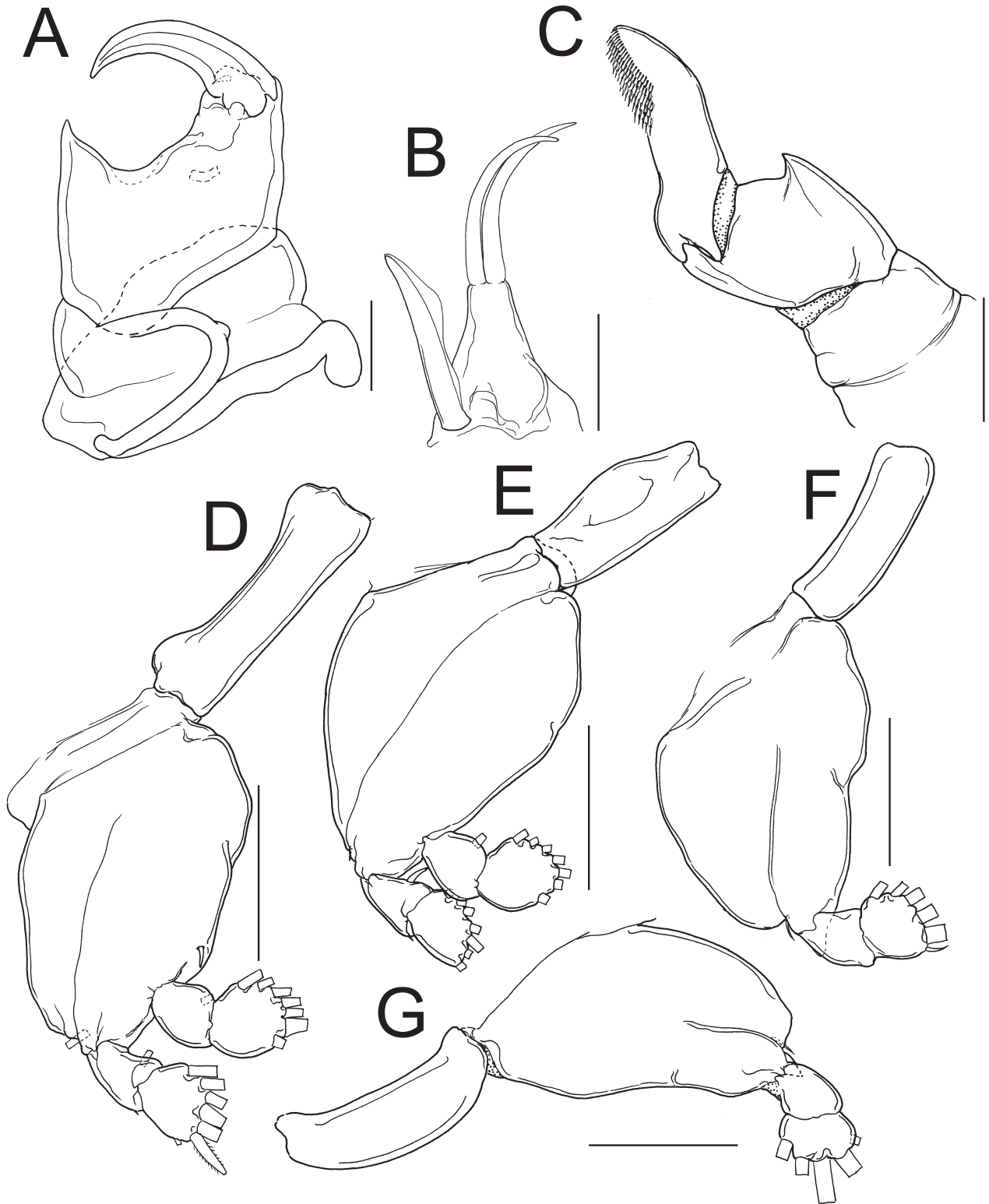


FIGURE 10. *Creopelates lubangensis* n. sp., postmetamorphic adult female, holotype, NMCR 39115. A, right antenna, anterior; B, left maxillule; C, left maxilla, anterior; D, right leg 1 with intercoxal sclerite, anterior; E, right leg 2 with intercoxal sclerite, anterior; F, right leg 3 with intercoxal sclerite, anterior; G, left leg 4 with intercoxal sclerite, anterior. Scale bars: A–C, 20 μ m; D, E, 50 μ m; F, G, 30 μ m.

Description of postmetamorphic adult female. Body (Fig. 9A) 5.24 long, comprising cephalothorax, neck region and trunk; junction of neck and trunk curved. Cephalothorax (Fig. 9A–C) ovoid, 0.35×0.37 , bearing paired

rounded antennary process with inner spherical projection and posterolateral lobes both with digitate fringes; ventral surface with irregularly situated small conical protrusions; rostrum (Fig. 9D) protruding. Neck region (Fig. 9A) narrow, with paired lateral digitate lobes, constriction in anterior $\frac{1}{3}$, with multiple posterior protrusions, fringed with series of about ten pairs of finely digitate lobes (Fig. 9A); second and third pedigers indistinctly segmented (Fig. 9B, C). Trunk (Fig. 9A, E) bean-shaped, longer than wide 2.13×1.42 , with anterior end narrowing slightly towards neck region. Abdomen conical, bearing median depression, located between oviducal pores (Fig. 9A, E). Egg-sac uniseriate, coiled (Fig. 9A).

Antennule (Fig. 9F) unsegmented, bearing 19 setae on anterior margin: distal tip with 10 setae distally, 2 of which share common base, and 1 aesthetasc. Antenna (Fig. 10A) 3-segmented, chelate, typical pennellid; proximal segment bearing; middle segment bearing one pointed protrusion on inner medial margin; terminal segment claw-like bearing small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 10B) comprising one blunt, flanged seta and lobe with two distal setae. Maxilla (Fig. 10C) 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment elongate, incompletely subdivided, with distal part ornamented with rows of small spinules. Maxilliped absent.

Legs 1 and 2 (Fig. 10D, E) biramous. Legs 3 and 4 (Fig. 10F, G) uniramous. Legs 1–4 evenly arrayed along posterior part of cephalothorax to neck region (Fig. 9C). Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	1–0	0–0; 5	Absent

Protopods of legs 1–4 connected to respective intercoxal sclerites (Fig. 10D–G).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk behind the base of the pectoral fin and attached to the vertebrae, while its trunk and egg sacs remained external to the fish's body wall (Fig. 6C, D).

Variability of female morphology. The morphology of the female paratype is as in the holotype. The measurements of the paratype are as follows ($n = 1$): body length 4.57; cephalothorax length 0.38; cephalothorax width 0.35; trunk length 1.96; trunk width 1.30.

Remarks. *Creopelates lubangensis* n. sp. differs from *C. floridus*, *C. hoshinoi* n. sp. and *C. shirakawai* n. sp. in having antennary processes with digitate fringes (vs. without digitate fringes). The copepod is distinguishable from *C. nohmijimensis* by the following character states: antennary processes with inner spherical process (vs. without such a process); the cephalothorax and neck region bearing several small conical processes (vs. without such processes); the neck region bearing multiple protrusions posteriorly (vs. without such protrusions).

Etymology. The specific name “*lubangensis*” refers to the locality where it was found, Lubang Island.

Creopelates sp.

Haemobaphes dilectus: Leigh-Sharpe, 1934, p. 38–39

Remarks. The copepod was described by Leigh-Sharpe (1934) based on three postmetamorphic adult females collected from *Bathygobius cyclopterus* (Valenciennes) (as *Gobius variabilis*) (Perciformes: Gobiidae) on Ambon reef, Banda Sea, Indonesia as a species of the genus *Haemobaphes* Steenstrup & Lütken, 1861. One of the distinctive characters of *Creopelates* is the possession of the neck region fringed by at least one paired, finely digitate lobes; its presence in *H. dilectus* indicates that it is a member of *Creopelates*. According to Leigh-Sharpe (1934), all type specimens lacked the cephalothorax and most of the neck region. Hence, it is impossible to identify the species and I recommend, therefore, that *Haemobaphes dilectus* is transferred to *Creopelates* as a *species inquirendum*.

Key to the species of *Creopelates*

(postmetamorphic adult females)

- 1 Antennary processes with digitate, branching fringes 2
- Antennary processes without digitate, branching fringes 3
- 2 Cephalothorax bearing small conical processes on ventral surface; antennary process with one knob-like inner accessory process; neck region bearing posterior multiple protrusions *C. lubangensis* n. sp.
- Cephalothorax without processes on ventral surface; antennary process without knob-like inner accessory process; neck region without posterior multiple protrusions *C. nohmijimensis*
- 3 Cephalic lobe small without digitate fringes; neck region fringed with one pair of finely digitate lobes *C. hoshinoi* n. sp.
- Cephalic lobe with digitate fringes; neck region fringed with series of about ten pairs of finely digitate lobes..... 4
- 4 Cephalothorax rectangular; cephalic lobe with small digitate fringes; leg 4 separated by gap from preceding legs; protopods of legs 3 and 4 separated from respective intercoxal sclerites by long gaps..... *C. floridus*
- Cephalothorax round; cephalic lobe with digitate, branching fringes; leg 4 not widely spaced from preceding legs; protopods of legs 3 and 4 connecting to respective intercoxal sclerites. *C. shirakawai* n. sp.

Genus *Nagasawanus* n. gen.

Diagnosis of postmetamorphic adult female. Body long, comprising cephalothorax, neck region and trunk; junction of neck and trunk slightly curved. Cephalothorax bearing paired round antennary processes and paired smooth spherical posterolateral lobes; rostrum projecting, narrow. Neck region narrow, curved near junction with trunk; second and third pedigers clearly segmented. Trunk pyriform, longer than wide, with anterior end narrowing towards neck region. Abdomen conical, located between oviducal pores. Egg-sac uniseriate, coiled or curved.

Antennule unsegmented, bearing more than 28 setae and 1 distal aesthetasc, 2 of distal setae sharing common base. Antenna 3-segmented, chelate, typical pennellid; proximal segment unarmed; middle segment bearing one pointed protrusion on inner medial margin, terminal segment claw-like bearing small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule bilobate, composed of knob-like lobes; inner lobe bearing one seta; outer lobe bearing two setae. Maxilla 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment forming elongate claw, incompletely subdivided. Maxilliped absent.

Legs 1 and 2 biramous. Legs 3 and 4 uniramous. Legs 1–4 evenly arrayed along posterior part of cephalothorax to neck region. Armature formula of legs 1–4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1–1	1–1; 7	0–1; 7
Leg 2	1–0	1–1; 7	0–1; 7
Leg 3	1–0	0–0; 6	Absent
Leg 4	0–0	0–0; 5	Absent

Adult male. Unknown.

Type species. *Nagasawanus akinohama* n. sp. by original designation.

Remarks. *Nagasawanus* n. gen. clearly differs from other pennellid genera by its possession of the following combination of characters: antennary processes and cephalic lobes rounded without branched fringes; neck region without any processes; maxilla with claw-like terminal segment without spinules.

Etymology. The generic name “*Nagasawanus*” is dedicated to Prof. Kazuya Nagasawa, an outstanding aquatic parasitologist.

Nagasawanus akinohama n. sp.

New Japanese name: Naga-wakizashi for both the genus and the species
(Figs 11A, 12, 13)

Type material. Holotype: postmetamorphic adult female (NSMT-Cr 23844) (dissected), ex *Trimma grammistes* (Tomiya) (Perciformes: Gobiidae), off Akinohama (34°47'N, 139°23'E), Izu-Oshima Island, Tokyo, North Pacific Ocean, Japan, 3 April 2011, leg. O. Hoshino. Paratype: 1 postmetamorphic adult female (NSMT-Cr 23845),

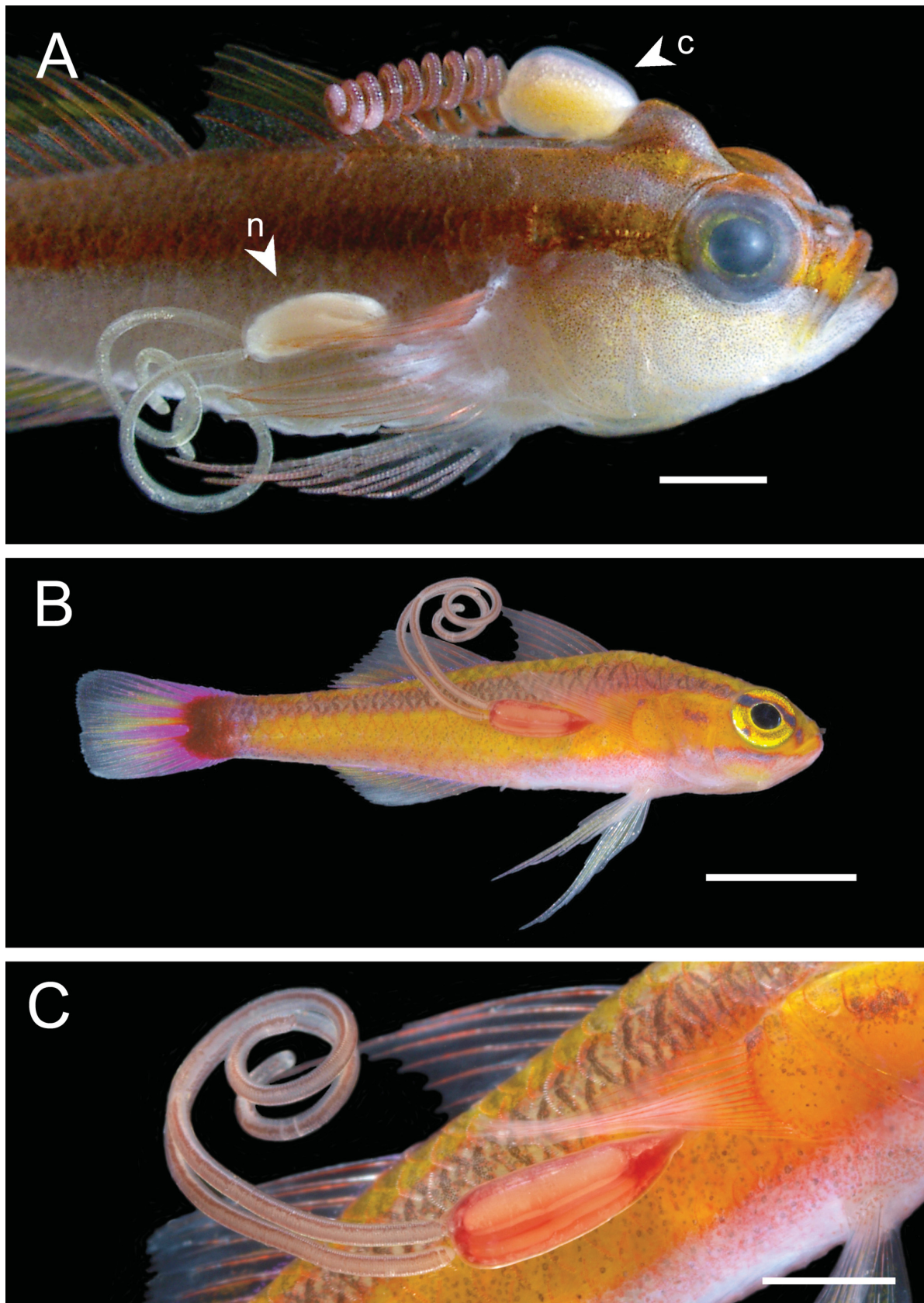


FIGURE 11. Postmetamorphic adult females of *Nagasawanus akinohama* n. gen. et n. sp. (A) and *N. snufkini* n. sp. (B, C) attached to their hosts. A, a specimen of *Trimma grammistes* (Tomiyama) infected by the paratype female (NSMT-Cr 23845), c = a female specimen of *Cardiodectes asper* Uyeno & Nagasawa, 2010, n = paratype female of *N. akinohama* n. gen. et n. sp.; B, a specimen of *Trimma tevegae* Cohen & Davis infected by a specimen of *N. snufkini*. C, coloration in life of a specimen attached to host's body. Scale bars: A, C, 2 mm; B, 5 mm.

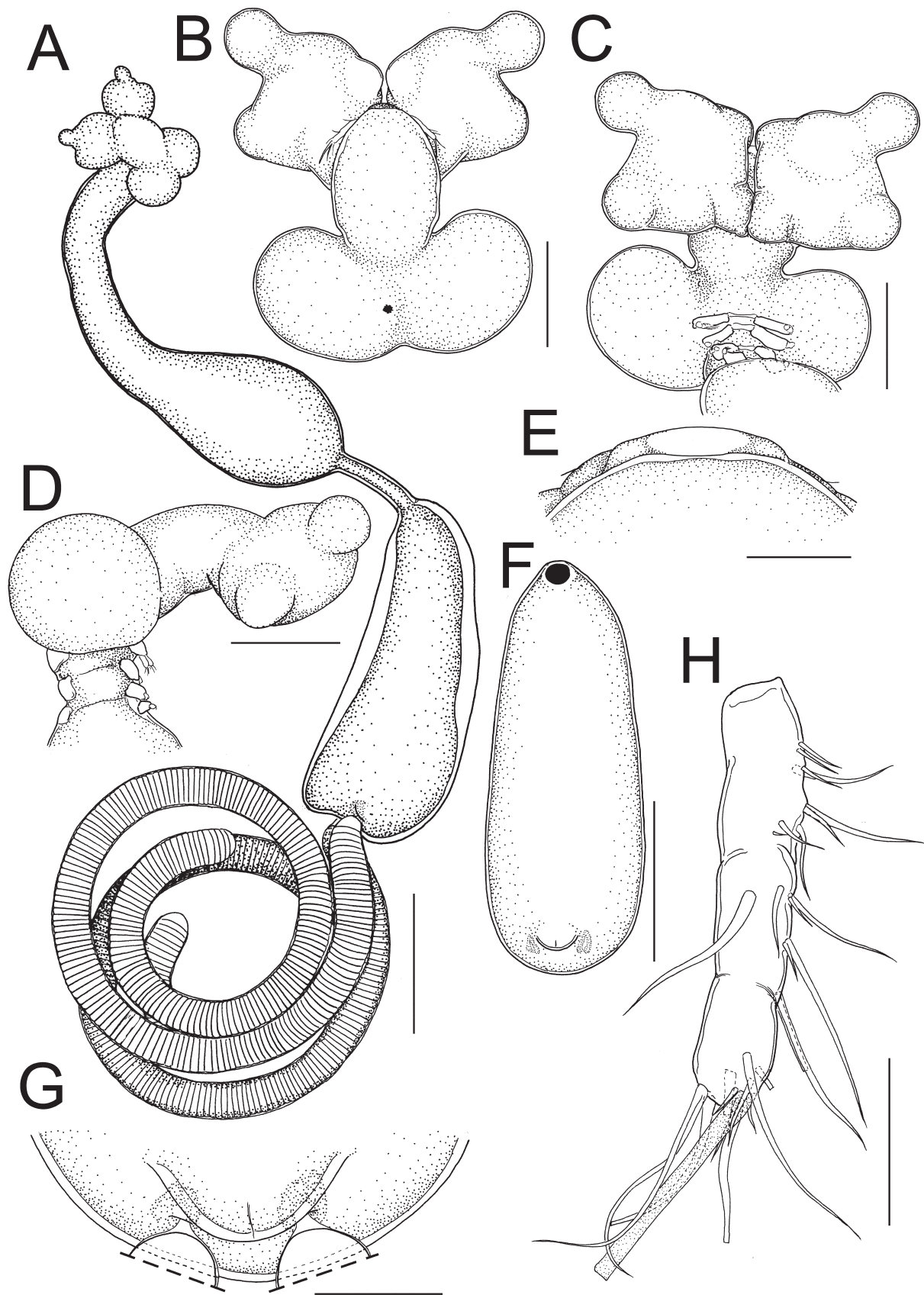


FIGURE 12. *Nagasawanus akinohama* n. gen. et n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23844. A, habitus; B, cephalothorax and anterior end of neck region, dorsal; C, same, ventral; D, same, lateral; E, anterior part of cephalothorax with rostrum; F, trunk, ventral; G, posterior part of trunk, ventral; H, right antennule, anterior. Scale bars: A, F, 1000 μ m; B–D, G, 250 μ m; E, 50 μ m; H, 30 μ m.

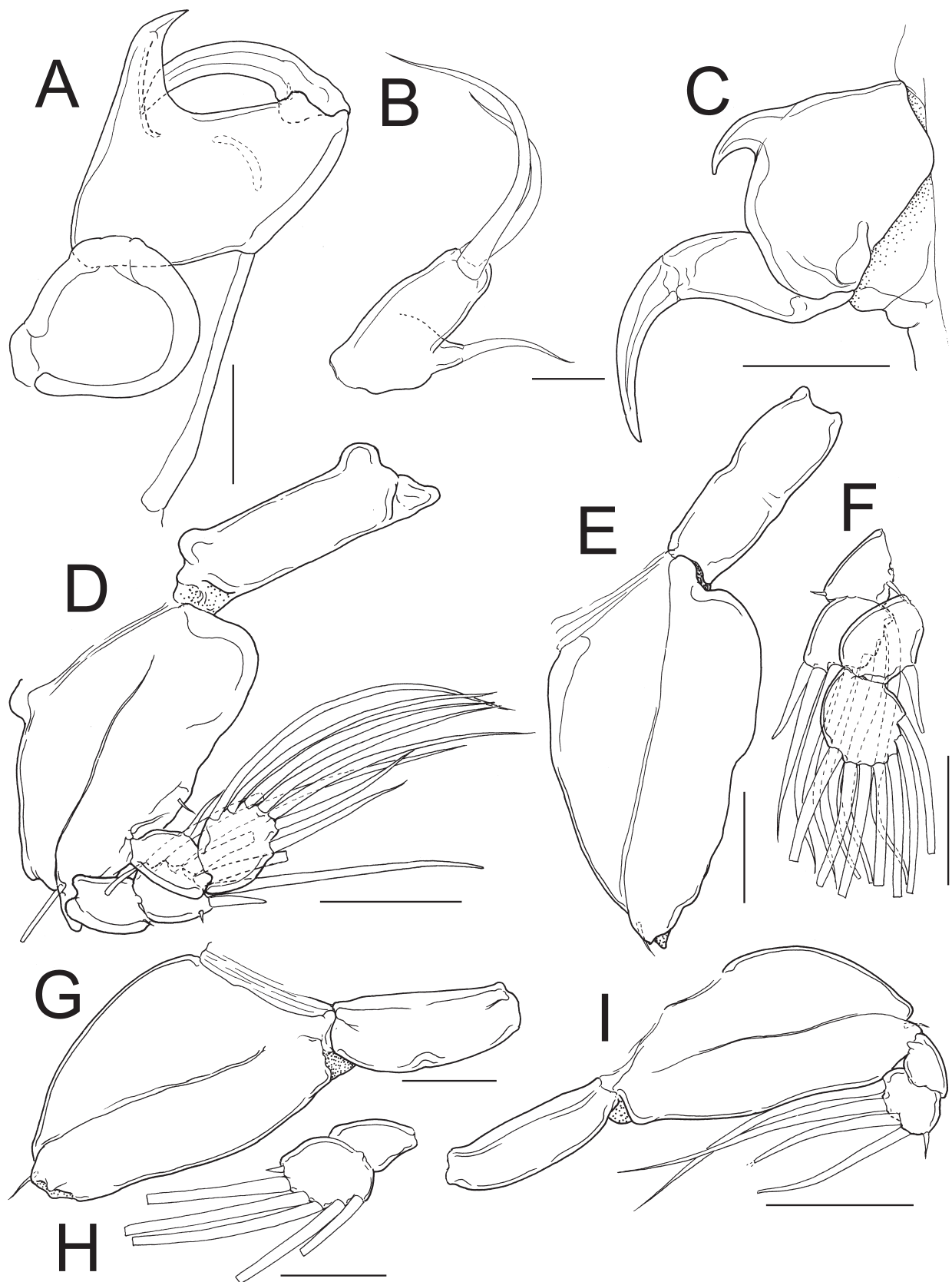


FIGURE 13. *Nagasawanus akinohama* n. gen. et n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23844. A, right antenna, anterior; B, left maxillule; C, left maxilla, anterior; D, right leg 1 with intercoxal sclerite, anterior; E, protopod of right leg 2 with intercoxal sclerite, anterior; F, rami of right leg 2 anterior; G, protopod of right leg 3 with intercoxal sclerite, anterior; H, exopod of right leg 3, anterior; I, left leg 4 with intercoxal sclerite, anterior. Scale bars: A, C, D–F, I, 30 μ m; B, 10 μ m; G, H, 20 μ m.

ex *T. grammistes*, off Akinohama (34°47'N, 139°23'E), Izu-Oshima Island, Tokyo, North Pacific Ocean, Japan, 30 m depth, 13 February 2011, leg. O. Hoshino; 1 postmetamorphic adult female (NSMT-Cr 23846), ex *T. grammistes*, off Akinohama (34°47'N, 139°23'E), Izu-Oshima Island, Tokyo, North Pacific Ocean, Japan, 40 m depth, 12 September 2013, leg. O. Hoshino.

Description of postmetamorphic adult female. Body (Fig. 12A) 6.89 long, comprising cephalothorax, neck region and trunk; junction of cephalothorax and neck bending through 90°; junction of neck and trunk curved. Cephalothorax (Fig. 12A–D) longer than wide 0.38×0.26 , bearing paired antennary processes and rounded posterolateral lobes; antennary process with additional spherical protrusion and three rounded smaller protrusions; rostrum (Fig. 12E) narrow. Neck region (Fig. 12A) narrow, curved near junction to cephalothorax with subterminal bulging and posterior constricted part; second and third pedigers clearly segmented (Fig. 12D). Trunk (Fig. 12A, F) pyriform, longer than wide 2.58×1.00 , with anterior end narrowing towards neck region. Abdomen conical, located between oviducal pores (Fig. 12A, F, G). Egg-sac uniseriate, coiled (Fig. 12A).

Antennule (Fig. 12H) unsegmented, bearing at least 17 setae on anterior margin: distal tip 11 setae distally, 2 of which sharing common base, and 1 aesthetasc. Antenna (Fig. 13A) 3-segmented, chelate, typical pennellid; proximal segment unarmed; middle segment bearing one pointed protrusion along inner medial margin, terminal segment claw-like bearing small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 13B) bilobate, composed of knob-like lobes; inner lobe bearing one seta; outer lobe bearing two setae. Maxilla (Fig. 13C) 2-segmented; proximal segment bearing single subterminal pointed process; terminal segment elongated claw, incompletely 2-segmented without ornamentation. Maxilliped absent.

Legs 1 and 2 (Fig. 13D–F) biramous. Legs 3 and 4 (Fig. 13G–I) uniramous. Legs 1 to 4 evenly arrayed along posterior part of cephalothorax to neck region (Fig. 12C). Armature formula of legs as for generic diagnosis.

Protopods of legs 1 to 4 connected to respective intercoxal sclerites (Fig. 13D, E, G, I).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk behind the base of the pectoral fin and attached to the vertebrae, while its trunk and egg sacs remained external to the fish's body wall (Fig. 11A).

Variability of female morphology. The morphology of the female paratypes are as in the holotype. The measurements of paratypes are as follows ($n = 2$): body length 8.11–9.32 (8.71 ± 0.86); cephalothorax length 0.35–0.42 (0.38 ± 0.05); cephalothorax width 0.28–0.34 (0.31 ± 0.04); trunk length 2.81–3.20 (3.00 ± 0.28); trunk width 1.11–1.24 (1.18 ± 0.09).

Etymology. The specific name of the new species, *akinohama*, refers to the type locality, Akinohama on Izu Oshima Island, North Pacific Ocean, Japan.

***Nagasawanus snufkini* n. sp.**

New Japanese name: Shin-no-wakizashi
(Figs 11B, C, 14, 15)

Type material. Holotype: postmetamorphic adult female (NSMT-Cr 23847) (dissected), ex *Trimma tevegae* Cohen & Davis (Perciformes: Gobiidae), off Oura Bay (26°32'N, 128°3'E), Okinawa-jima Island, Ryukyu Islands, North Pacific Ocean, Japan, 10 m depth, 28 January 2014, leg. D. Uyeno, S. Nishihira, and M. Arai. Paratype: 1 postmetamorphic adult female (NSMT-Cr 23848), ex *T. tevegae*, off Oura Bay (26°32'N, 128°3'E), Okinawa-jima Island, Ryukyu Islands, North Pacific Ocean, Japan, 13 m depth, 19 February 2012, leg. D. Uyeno and S. Nishihira; 1 postmetamorphic adult female (NSMT-Cr 23849) (dissected), ex *T. tevegae*, off Oura Bay (26°32'N, 128°3'E), Okinawa-jima Island, Ryukyu Islands, North Pacific Ocean, Japan, 14 m depth, 20 October 2013, leg. D. Uyeno and S. Nishihira; 1 postmetamorphic adult female (RUMF-ZC-3679), ex *T. tevegae*, off Oura Bay (26°32'N, 128°3'E), Okinawa-jima Island, Ryukyu Islands, North Pacific Ocean, Japan, 14 m depth, 20 October 2013, leg. D. Uyeno and S. Nishihira.

Description of postmetamorphic adult female. Body (Fig. 14A) 6.39 long, comprising cephalothorax, neck region and trunk; junction of neck and trunk curved. Cephalothorax (Fig. 14A–D) longer than wide 0.53×0.41 , bearing paired rounded antennary process with small additional rounded protrusions and posterolateral lobes; rostrum (Fig. 14E) narrow, with curved frontal margin. Neck region (Fig. 14A) curved in anterior $\frac{1}{3}$, narrowing

slightly towards trunk; second and third pedigers clearly segmented (Fig. 14B, D). Trunk (Fig. 14A, F) pyriform, longer than wide 2.80×0.81 , with anterior end narrowing towards neck region. Abdomen conical, bearing median depression, located between oviducal pores (Fig. 14A, F, G). Egg-sac uniseriate, curved in single plane (Fig. 14A).

Antennule (Fig. 14H) unsegmented, bearing 21 setae on anterior margin: distal tip 11 setae distally, 2 of which sharing common base, and 1 aesthetasc. Antenna (Fig. 15A) 3-segmented, chelate, typical pennellid; proximal segment unarmed; middle segment bearing one pointed protrusion on inner medial margin, terminal segment claw-like bearing small basal element on posterior surface. Mouth tube, maxillule, and maxilla located near base of antenna on anterior part of ventral surface of cephalothorax. Maxillule (Fig. 15B) bilobate, composed of knob-like lobes; inner lobe bearing one seta; outer lobe bearing two setae. Maxilla (Fig. 15C) 2-segmented; proximal segment bearing single subterminal pointed long process; terminal segment forming elongate claw with one row of teeth-like processes along posterior margin. Maxilliped absent.

Legs 1 and 2 (Fig. 15E) biramous. Legs 3 and 4 (Fig. 15G) uniramous. Legs 1 to 4 evenly arrayed along posterior part of cephalothorax to neck region (Fig. 14C). Armature formula of legs as follows:

	Protopod	Exopod	Endopod
Leg 1	broken	broken	broken
Leg 2	1-0	1-1; 7	0-1; 7
Leg 3	broken	broken	broken
Leg 4	1-0	broken	Absent

Protopods of legs 1 to 4 connected to respective intercoxal sclerites (Figs 14C, 15E, G).

Attachment site. The cephalothorax and neck of the copepod were embedded in the musculature of the host's trunk posterior to the base of the pectoral fin and attached to the vertebrae, while its trunk and egg sacs remained external the fish's body wall (Fig. 11B, C).

Variability of female morphology. The morphology of the female paratypes is as in the holotype. Armature formula of legs 1 and 3 of paratypes (Fig. 15D, F) as follows:

	Protopod	Exopod	Endopod
Leg 1	1-1	1-1; 7	0-1; 7
Leg 3	1-0	0-0; 6	absent

Measurements of paratypes as follows ($n = 3$): body length 6.18–7.25 mm (6.84 ± 0.58); cephalothorax length 0.44–0.65 (0.56 ± 0.11); cephalothorax width 0.33–0.35 (0.34 ± 0.02); trunk length 2.62–2.90 (2.76 ± 0.20); trunk width 0.73–0.93 (0.83 ± 0.14).

Remarks. *Nagasawanus snufkini* n. sp. clearly differs from its congener *N. akinohama* n. sp. by the following character states: cephalothorax connecting along linear axis to second pedigerous somite (vs. connecting via 90° flexure to second pedigerous somite); antennary processes with a small additional rounded protrusion (vs. with four additional protrusions); neck region without constricted, narrowed section (vs. with posterior constriction); maxilla with terminal segment with a serrated margin (vs. with a smooth margin) in postmetamorphic adult female.

Etymology. The specific name of the new species, *snufkini*, refers to the nickname of Mr. Shin Nishihira, the founder of the Diving Team Snuck Snufkin, who is the best explorer of Oura Bay, Okinawa-jima Island, Japan.

Key to species of *Nagasawanus* (postmetamorphic adult females)

- 1 Cephalothorax bearing anterolateral lobes with one anterior and two posterior pairs of rounded processes; junction of cephalothorax and neck bending through 90°; maxilla bearing elongate second segment with smooth margin *N. akinohama* n. gen. et n. sp.
- Cephalothorax bearing anterolateral lobes with one pair of posterior rounded processes; junction of cephalothorax and neck straight; maxilla bearing elongate second segment with serrated margin. *N. snufkini* n. gen. et n. sp.

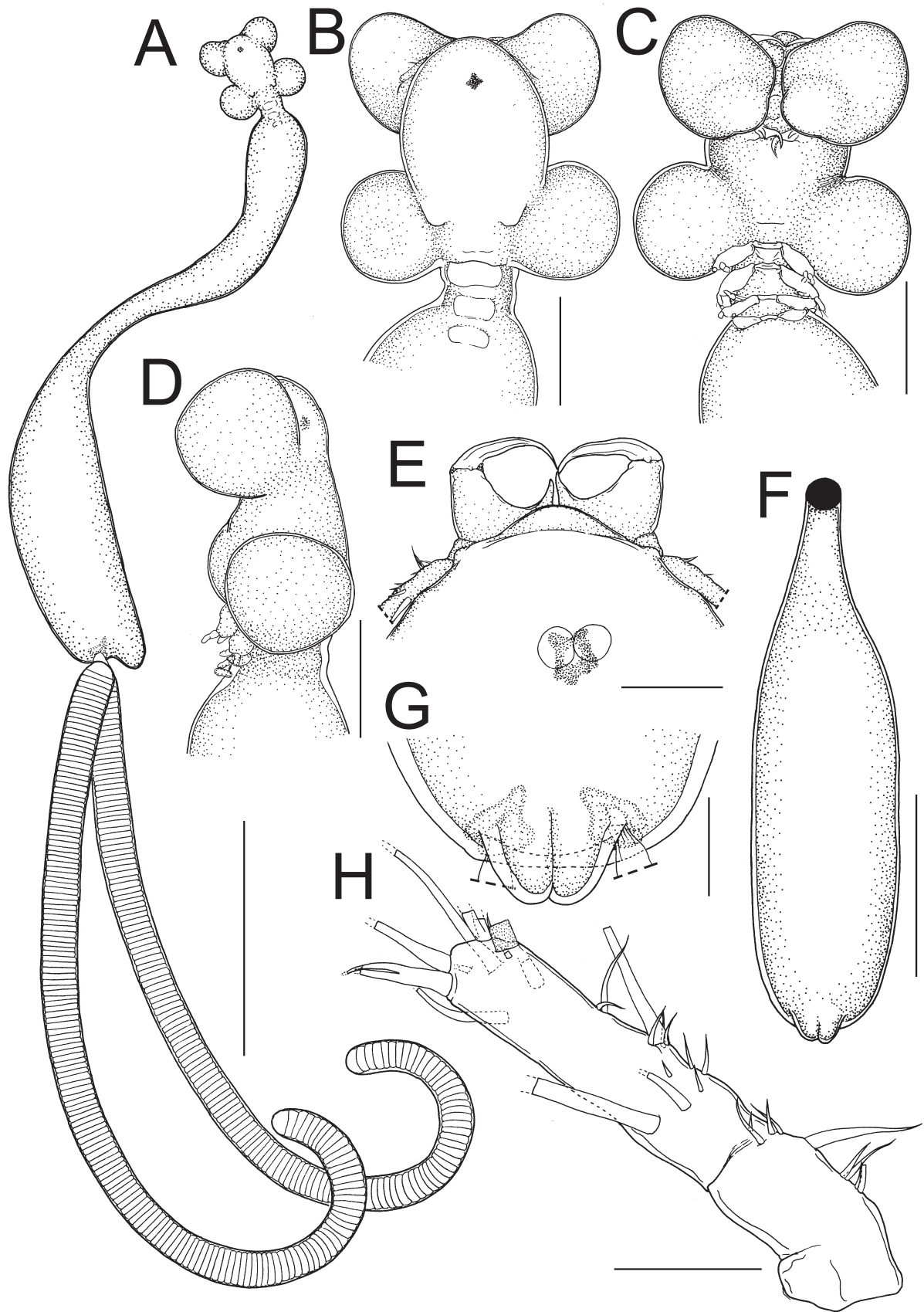


FIGURE 14. *Nagasawanus snufkini* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23847. A, habitus; B, cephalothorax and anterior end of neck region, dorsal; C, same, ventral; D, same, lateral; E, anterior part of cephalothorax with rostrum; F, trunk, ventral; G, posterior part of trunk, ventral; H, left antennule, anterior. Scale bars: A, 2000 µm; B–D, 300 µm; E, 100 µm; F, 1000 µm; G, 200 µm; H, 30 µm.

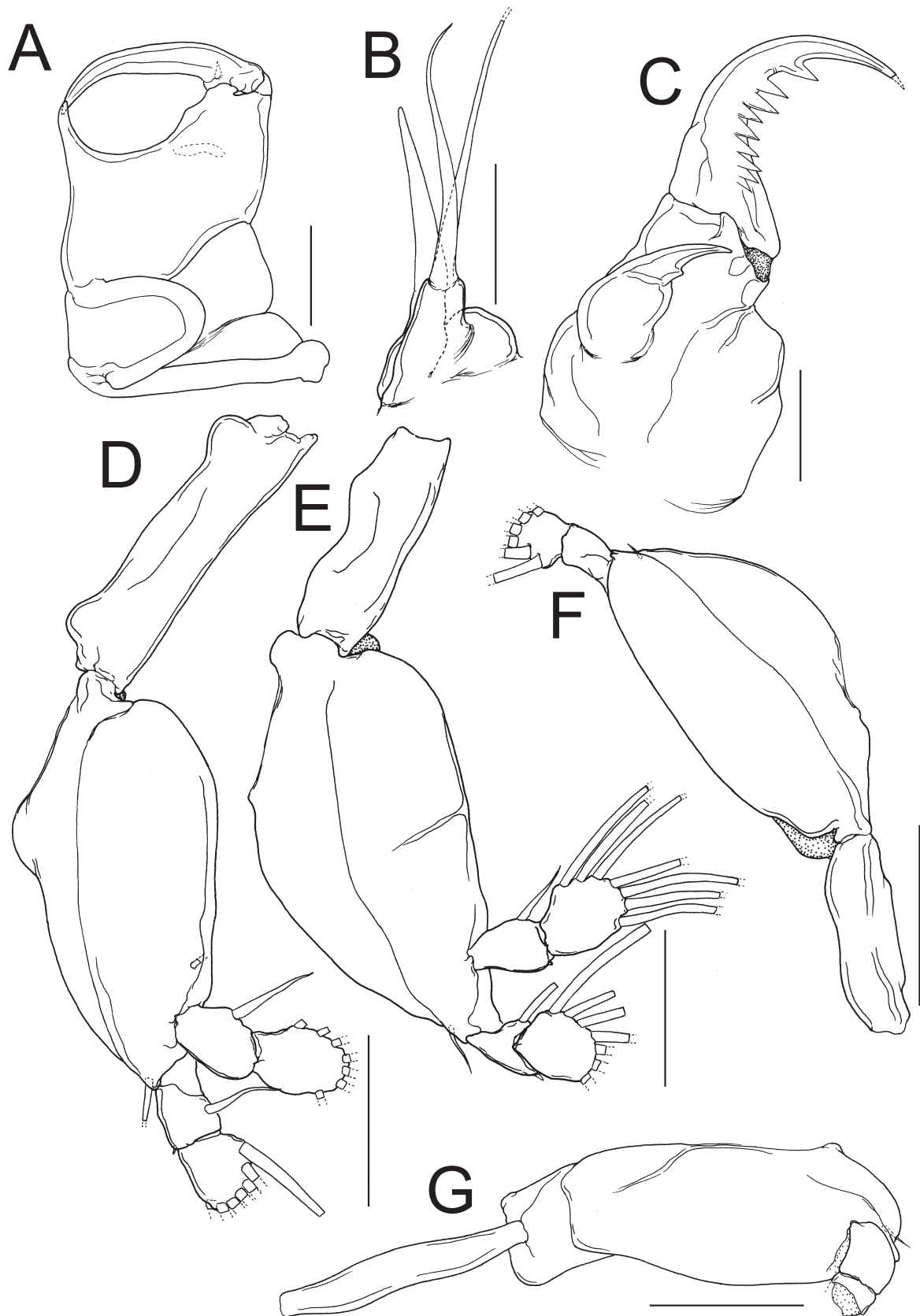


FIGURE 15. *Nagasawanus snufkini* n. sp., postmetamorphic adult female, holotype, NSMT-Cr 23847 (A–C, E, G), paratype, NSMT-Cr 23849 (D, F). A, right antenna, anterior; B, left maxillule; C, right maxilla, anterior; D, right leg 1 with intercoxal sclerite, anterior; E, right leg 2 with intercoxal sclerite, anterior; F, right leg 3 with intercoxal sclerite, anterior; G, left leg 4 with intercoxal sclerite, anterior. Scale bars: A, D–F, 50 μ m; B, C, G, 30 μ m.

Discussion

According to Boxshall's (1986) analysis, *Creopelates* Shiino, 1948 is associated with the *Phrixocephalus*-group which includes four genera (*Impexus* Kabata, 1972, *Peroderma* Heller, 1865, *Phrixocephalus* Wilson C.B., 1908, and *Serpentisaccus* Blasiola, 1979), characterized by the following synapomorphic character states: holdfast set at angle to longitudinal axis of trunk; antennary processes present; neck incorporating metasome; cephalic lateral lobes present. *Nagasawanus* n. gen. is a member of this group by virtue of sharing all these characters. In addition, the new genus is considered to be most closely related to *Creopelates* by sharing the following characters: long neck; antennary processes and lateral lobes well developed; lacking additional lateral lobes on cephalothorax. However, *Nagasawanus* n. gen. is clearly distinguished from *Creopelates* by having an unarmed neck region (*vs.* neck fringed with series of finely digitate lobes in *Creopelates*) and the maxilla has the claw-like terminal segment unornamented (*vs.* terminal segment bearing round tip covered with rows of spinules in *Creopelates*) (see Shiino 1958; Uyeno & Nagasawa 2010b; present study).

Boxshall (1986) placed *Cardiodectes* Wilson, 1917 in the adjacent clade to the *Phrixocephalus*-group, distinguished because its holdfast is not set at an angle to the longitudinal axis of the trunk. Currently, 16 species of *Cardiodectes* are now known, and at least four of them (*C. asper* Uyeno & Nagasawa, 2010, *C. bellwoodi* Uyeno, 2013, *C. bertrandi* Uyeno & Nagasawa, 2010, *C. shinni* Uyeno, 2013) are known to have the neck set at an angle to the trunk (Uyeno & Nagasawa 2010b; Uyeno 2013). When Kabata (1972) established *Impexus* based on *I. hamondi* Kabata, 1972, he pointed out that *Cardiodectes* differs from *Impexus* as follows: egg sacs loosely coiled or not coiled; trunk cylindrical and connected to neck at distal end. Furthermore, the two pairs of cephalic lobes present in *Impexus* were deemed as a unique character of this genus. However, *C. bellwoodi*, *C. asper* and *C. shinni* also have distinct spirally-coiled egg sacs and the neck connects to the near distal part of the trunk (see Uyeno & Nagasawa 2010b; Uyeno 2013). Also, *C. asper* and *C. shinni* have a pair of lateral lobes positioned behind the level of leg 2 on the neck, and these lobes are probably homologous with the inner pair of lobes located behind a thoracopod (possibly leg 1) of *I. hamondi*. Consequently only the trunk with a flat ventral surface and a protruding posterior part (abdomen, probably) remain as potential diagnostic characters of *Impexus*. Since no information was provided on the morphology and numbers of appendages in the original description (Kabata 1972), a full redescription of *I. hamondi* is needed in order to confirm its validity and determine its phylogenetic affinities.

Blasiola (1979) established *Serpentisaccus*, another monotypic genus of the *Phrixocephalus*-group, based on *S. magnificus* Blasiola, 1979. *Serpentisaccus* is similar to *Peroderma* Heller, 1865 but it can be differentiated by having the trunk subdivided into swollen anterior and smaller posterior parts and by the zigzag-shaped egg sacs (see Izawa 1977; Blasiola 1979). Although *S. magnificus* was depicted as having a subdivided trunk in the illustrations of the original description (Blasiola 1979, fig. 1, 2, 4), observation of additional specimens revealed that the trunk is simply constricted but not segmented (Uyeno *et al.* 2013). Further morphological study including a redescription of *S. magnificus* is needed to clarify differences between *Serpentisaccus* and *Peroderma*.

As described above, boundaries between pennellid genera are unclear in some cases. In order to validate each genus, redescriptions of all established genera that are poorly known, is needed. Phylogenetic studies based on molecular analyses will provide new evidence necessary to resolve some of the problems.

In this and previous studies, the author examined fresh specimens of all valid species of *Creopelates* and *Nagasawanus* attached to their hosts, except *C. floridus* (Uyeno & Nagasawa, 2010b; present study). With *C. floridus*, all fixed host specimens were preserved with copepods. Hosts are typically infected by only one or two copepod specimens; in one case one individual of *Trimma tevegae* carried three specimens of *N. snufkini* n. sp. The author has also observed many individuals of *T. tevegae* infected by *N. snufkini* n. sp. in the field but they are usually infected by a single or only two copepods. Many examples of the negative impact on the hosts by pennellids have been reported (e.g., Kabata & Forrester 1974; Nagasawa & Maruyama 1986; Becheikh *et al.* 1997). Since all known species of both *Creopelates* and *Nagasawanus*, except *C. hosinoi* n. sp., are considered to feed directly on the host's blood from the dorsal artery or vein, the negative impact on the host caused by the copepods is probably serious. Consequently, an infection of more than three individuals of copepods on a single host might be regarded as fatal.

In the last two decades, 18 new species of pennellids have been described, and the fisheries value of almost all of their known hosts is low (Kazachenko 1995; Ho *et al.* 2007; Uyeno & Nagasawa 2010a, b; Moon & Choi 2014; Uyeno *et al.* 2012; Uyeno 2013; present study). Of these species, 14 have been collected during field surveys by

SCUBA divers (Uyeno & Nagasawa 2010a, b; Uyeno 2013; present study). Also, two known species from low value fishes are newly recorded in Japan (Uyeno *et al.* 2013, 2014). Most of the well-studied parasitic copepods on fish have been found on commercially important fishes. To reveal the real diversity of these copepods, future studies should be focused on non-commercial fishes and field surveys are urgently needed. Even though *T. tevegae*, a host of *N. snufkini* n. sp., is a common species in the Ryukyu Islands, this copepod have never been found on other populations living outside of Oura bay, the type locality, in Okinawa-jima Island despite numerous field surveys conducted over the past five years. This might indicate that pennellid species may be restricted to limited geographical ranges.

Key to genera of Pennellidae

(postmetamorphic adult females)

1	Abdomen with brush-like processes	2
-	Abdomen without processes	4
2	Cephalothorax bearing one pair of rod-like lateral processes	<i>Pennella</i>
-	Cephalothorax bearing one pair of branching processes or not elongate processes	3
3	Egg sacs spirally coiled	<i>Lernaeolophus</i>
-	Egg sacs linear	<i>Parinia</i>
4	Trunk sigmoid	5
-	Trunk not sigmoid	8
5	Neck region bearing one pair of lateral processes	<i>Haemobaphes</i>
-	Neck region without such structures	6
6	Cephalic process branched; egg sacs coiled irregularly	<i>Lernaeocera</i>
-	Cephalic process simple rod-like; egg sacs spirally coiled	7
7	Legs 1 to 3 biramous; leg 4 uniramous	<i>Trifur</i>
-	Legs 1 to 4 uniramous	<i>Allotrifur</i>
8	Antennary processes absent	9
-	Antennary processes present	13
9	Caudal rami present	10
-	Caudal rami absent	11
10	Trunk bearing one pair of long processes on posterolateral corner	<i>Peniculisa</i>
-	Trunk without long processes	<i>Peniculus</i>
11	Distinctly protruding proboscis present	12
-	Proboscis not protruding	<i>Lernaeenicus</i>
12	Cephalothorax without lateral processes; proboscis exceeding body length several times; neck region bearing one pair of lateral lobes	<i>Ophiolernaeae</i>
-	Cephalothorax bearing one pair of lateral processes with conical tip; proboscis not exceeding half of body length; neck region without lateral lobes	<i>Sarcotretes</i>
13	Antennary processes not plate-like	14
-	Antennary processes plate-like	<i>Exopenna</i>
14	Caudal rami present; antennary processes short and conical; cephalic lobe absent	15
-	Caudal rami absent; antennary processes not conical; cephalic lobe present	16
15	Proboscis protruding; leg 4 absent	<i>Metapeniculus</i>
-	Proboscis not protruding; leg 4 present	<i>Propeniculus</i>
16	Two pairs of cephalic lobes; trunk with flat ventral surfaces	<i>Impexus</i>
-	One pair of cephalic lobes; trunk with convex ventral surface	17
17	Short proboscis present	<i>Pseudopeniculus</i>
-	Proboscis not protruding	18
18	Trunk bearing posterior constriction; egg sacs zigzag shaped	<i>Serpentisaccus</i>
-	Trunk without posterior constriction; egg sacs not linear or spirally coiled	19
19	Neck region bearing more than one pairs of fringed lobes	<i>Creopelates</i>
-	Neck region without fringed lobes	20
20	Antennary process small, not lobe-like; cephalic process elongate, branched	<i>Phrixocephalus</i>
-	Antennary process lobe-like or globular; cephalic lobe round with branching digitate fringes or unarmed	21
21	Neck region connected at angle to ventral side; antennary process formed into elongate branched additional processes or without any additional processes	<i>Peroderma</i>
-	Neck region connected to distal or near distal part of trunk; lobe-like antennary processes with or without nodular and branching processes	22
22	Antennary processes lobe-like with nodular and branching processes	<i>Cardiodectes</i>
-	Antennary processes lobe-like without nodular and branching processes	<i>Nagasawanus</i> n. gen.

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