

Original Article

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Dirivultidae (Copepoda: Siphonostomatoida) from hydrothermal vent fields in the Okinawa Trough, North Pacific Ocean, with description of one new species

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Abstract

Two species of dirivultid copepod (Siphonostomatoida), *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013 and *Dirivultus kaiko* sp. nov., were discovered from hydrothermal vent fields in the Okinawa Trough, the western North Pacific. Since *S. senckenbergi* was originally described based on two adult males from the New Ireland Fore-Arc system, Papua New Guinea, the discovery here represents the second record. This species was attached on ventral setae covered with filamentous bacteria of the deep-sea squat lobster *Shinkaia crosnieri* (Decapoda: Munidopsidae). The female of *S. senckenbergi* is described for the first time as well as the nauplius I and the copepodid IV. Sexual dimorphism is shown on several appendages (i.e. antennule, leg 2 and leg 5). The nauplius I shows typical lethitrophic characteristics. *Dirivultus kaiko* sp. nov., which was found on the tentacular crown of the siboglinid tubeworm *Lamellibrachia columna*, differs from its two congeners by the antennule, maxilliped and leg 5 of both sexes. These are the second and third dirivultid species to be reported from Japan.

Introduction

The family Dirivultidae Humes & Dojiri, 1981 (Copepoda: Siphonostomatoida) is endemic to deep-water hydrothermal vent fields and hydrocarbon seeps and the surrounding axial summit trough (Humes, 1999; Gollner *et al.*, 2010; Ivanenko *et al.*, 2011). Currently, the family consists of 61 species of 12 genera. Many members have been found in residues after washings of terbellid polychaetes, gastropods, bivalves and decapods (Boxshall & Halsey, 2004; Gollner *et al.*, 2010), with few clearly defined hosts and sampling locations. Among this family, *Stygiopontius* Humes, 1987 consists of 27 species that have been recorded from both Pacific and Atlantic Oceans (Humes, 1987, 1989, 1990, 1991, 1996, 1997; Ivanenko *et al.*, 2006, 2011; Ivanenko & Ferrari, 2013; Uyeno *et al.*, 2018; Lee *et al.*, 2020). These species are concentrated in the Mid-Atlantic Ridge and the East Pacific Rise and its neighbouring and connecting ridges. Recently, four species were described from the Central Indian Ridge, Indian Ocean (Lee *et al.*, 2020). From the Western Pacific, six species are recorded (i.e. *S. brevispina* Humes, 1991 and *S. lauensis* Humes, 1991 from Lau Basin; *S. pectinatus* Humes, 1987 and *S. stabilitus* Humes, 1990 from Mariana Back-Arc Basin; *S. senckenbergi* Ivanenko & Ferrari, 2013 from the New Ireland Fore-Arc; and *S. senokuchiae* Uyeno, Watanabe & Shimanaga, 2018 from Izu-Bonin Arc) (Humes, 1990, 1991; Gollner *et al.*, 2010; Ivanenko & Ferrari, 2013; Uyeno *et al.*, 2018). In many species of the family, the morphology of adult stages was known, but the only developmental stages described were the nauplius I of *S. pectinatus*, the copepodid I of both *S. horridus* Lee, Kim & Kim, 2020 and an unidentified species, and the copepodid V of *Aphotopontius temperatus* Humes, 1997 (Humes, 1997; Ivanenko, 1998; Ivanenko *et al.*, 2007; Lee *et al.*, 2020).

In this study, two species of the family Dirivultidae are described from hydrothermal vent fields in the Okinawa Trough, the western North Pacific. Adult females and two developmental stages (nauplius I and copepodid IV) of *S. senckenbergi*, which was originally described by Ivanenko & Ferrari (2013) based on adult males from Papua New Guinea, are reported from the galatheid squat lobster *Shinkaia crosnieri* Baba & Williams, 1998 (Decapoda: Munidopsidae). *Dirivultus kaiko* sp. nov. is described based on adult females and males collected from the tentacular crown of the siboglinid tubeworm *Lamellibrachia columna* Southward, 1991.

Materials and methods

The copepod specimens were mainly collected during the research cruise (KR18-15), and also from other cruises (NT97-14, NT05-03 Leg. 2, NT10-E01, KR15-16, NT15-13, and KR16-16)



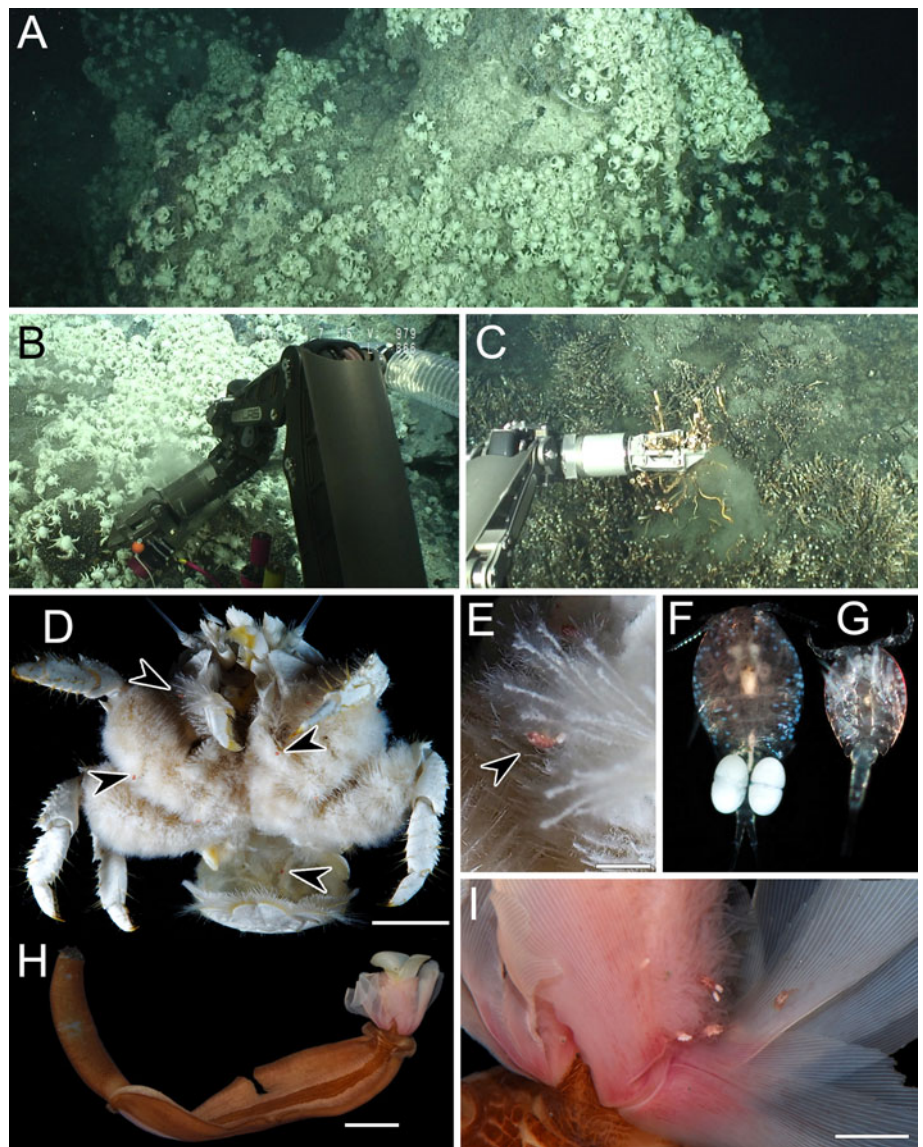


Fig. 1. Sampling sites at the Iheya North Knoll, Okinawa Trough and live colouration of animals. A, the sampling site of *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013 at a depth of 980 m. B, *Shinkaia crosnieri* Baba & Williams, 1998 collected by a suction sampler (Slurp Gun). C, *Lamellibrachia columna* Southward, 1991 collected by a manipulator at a depth of 987 m. D, *Sh. crosnieri* harbouring *S. senckenbergi*. E, *S. senckenbergi* on the ventral seta of the host. F, fresh specimen of *S. senckenbergi*, adult female (~1.2 mm in body length). G, same, adult male (~0.7 mm in body length). H, fresh specimen of *L. columna*. I, *Dirivultus kaiko* sp. nov. attached on the tentacular crown of *L. columna*. Arrowheads indicate copepods. Scale bars: D, H, 10 mm; E, 2 mm; I, 3 mm.

all conducted in hydrothermal vent fields of the Okinawa Trough (Figure 1A–C), East China Sea, the western North Pacific operated by the R/V ‘Kairei’ with the ROV ‘Kaiko 7000’ and ‘7000II’ and the R/V ‘Natsushima’ with the ROV ‘Hyper-Dolphin’ belonging to Japan Agency for Marine–Earth Science and Technology (JAMSTEC), Yokosuka, Japan. Deep-sea squat lobsters and tubeworms were collected using a suction sampler (Slurp Gun) and a manipulator installed on the ROV, respectively (Figure 1B, C). Copepods were removed from hosts and fixed and preserved in 99% ethanol for morphological and future molecular studies.

For morphological study, selected copepod specimens were subsequently soaked in lactophenol for 24 h, dissected by a sharpened tungsten needle under a dissecting microscope, and examined based on the modified version of the wooden slide method of Humes & Gooding (1964). Drawing were made with the aid of a drawing tube mounted on the biological microscope BX53 (Olympus, Tokyo, Japan) with differential interference contrast. Copepods were measured by an ocular micrometer, and measurements were given in μm as the range followed by the mean and standard deviation in parentheses. Types and other examined specimens are deposited in the crustacean collection of the National Museum of Nature and Science, Tsukuba, Japan (NSMT).

Results

Systematics

Dirivultidae Humes & Dojiri, 1980

Stygiopontius Humes, 1987

Stygiopontius senckenbergi Ivanenko & Ferrari, 2013
(Figures 1D–G, 2–9)

Stygiopontius senckenbergi Ivanenko & Ferrari, 2013,
pp. 1807–1812.

Materials Examined

Adult female (NSMT-Cr 28363), ex *Shinkaia crosnieri* (Decapoda: Munidopsidae), the Iheya North Knoll (27°47.371'N 126°53.843'E), off Okinawa Island, East China Sea, 980 m depth, 16 November 2018. Adult male (NSMT-Cr 28364), collection data same as that of NSMT-Cr 28363. 25 adult females and 26 adult males (NSMT-Cr 28365), collection data same as that of NSMT-Cr 28363. Five females and three males (NSMT-Cr 28366), ex *Sh. crosnieri* (Onboard ID: HD1859 BC1-12, collected at Aki site in Iheya North hydrothermal vent field, 27°46.007'N 126°54.188'E), off Okinawa Island, East China Sea, 1095 m depth, 1 August 2015; one female and one male (NSMT-Cr 28367), ex *Sh. crosnieri* (Onboard ID: KIV673 BC1-02, Ana site 26°13.3777'N 126°28.3017'E), off Okinawa Island, East China

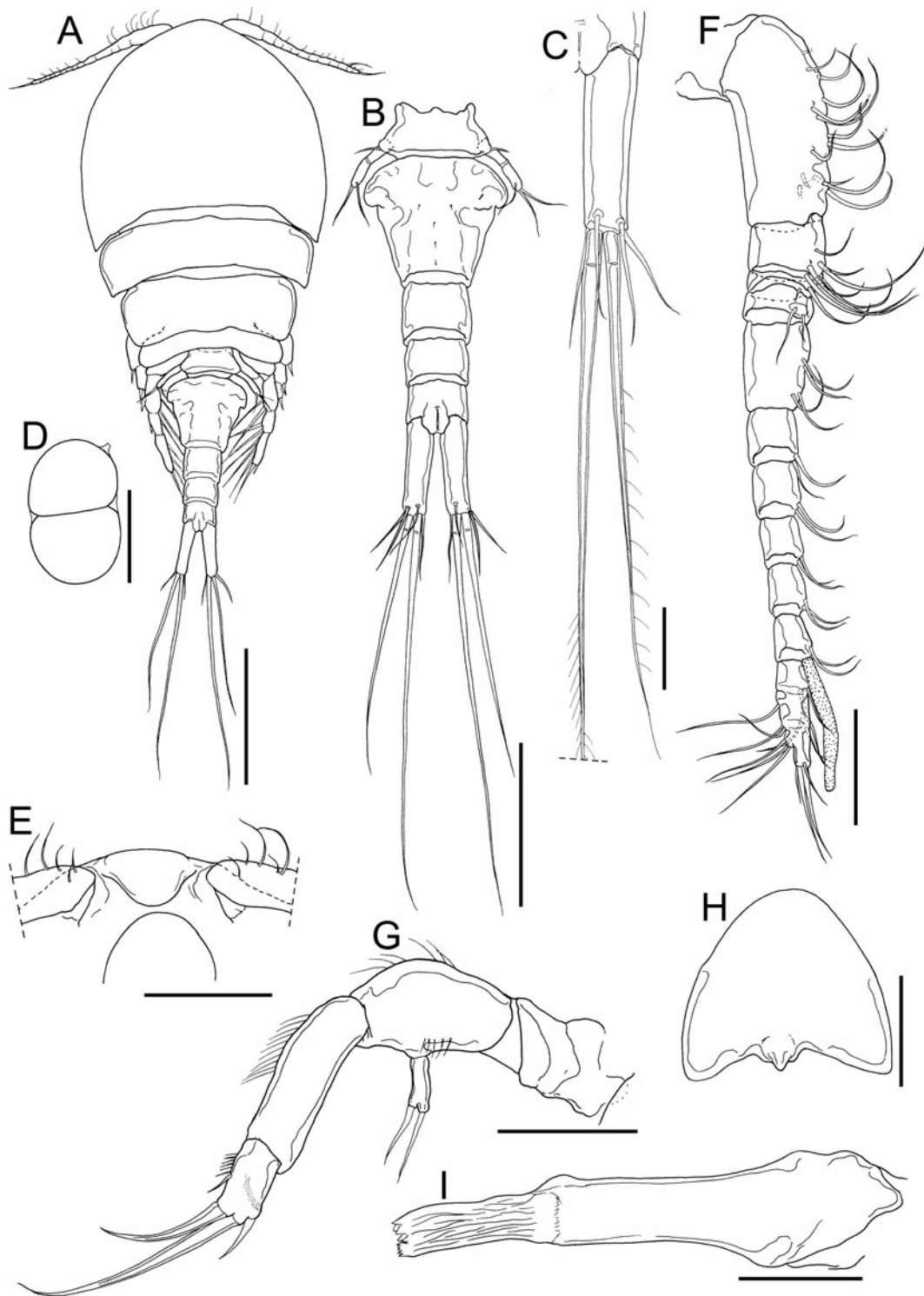


Fig. 2. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, adult female (NSMT-Cr 28363). A, habitus, dorsal; B, urosome, dorsal; C, right caudal ramus, dorsal; D, egg sac; E, rostral area, ventral; F, left antennule, posterior; G, left antenna, posterior; H, labrum; I, left mandible. Scale bars: A, 300 μ m; B, D, 200 μ m; C, F, G, H, 50 μ m; E, 100 μ m; I, 20 μ m.

Sea, 1085 m depth, 5 November 2015; nine females (NSMT-Cr 28368), ex *Sh. crosnieri* (Onboard ID: KIV717 BC1-3-1, Waka site in Futagoyama hydrothermal field, 24°52.0468'N 123°18.4832'E), off Okinawa Island, East China Sea, 1288 m depth, 21 November 2016; eight females (NSMT-Cr 28369), ex *Sh. crosnieri* (Onboard ID: KIV722 BC1-1, Gondo site, 26°18.4871'N 126°24.9294'E), off Okinawa Island, East China Sea, 1414 m depth, 1 December 2016; two females (NSMT-Cr 28370), ex *Sh. crosnieri*, the Izeha Hole (27°16.304'N 127°04.885'E), off

Okinawa Island, East China Sea, 1308 m depth, 22 April 2005; five females (NSMT-Cr 28371), ex *Sh. crosnieri*, the Hatoma Knoll (24°51.486'N 123°50.512'E), off Yaeyama Islands, East China Sea, 1480 m depth, 24 April 2005; five females (NSMT-Cr 28372), ex *Sh. crosnieri*, the North of Iheya Ridge (27°47.430'N 126°53.850'E), off Okinawa Island, East China Sea, 1023 m depth, 3 September 2010; six females (NSMT-Cr 28373), ex *Sh. crosnieri*, the Iheya North Field (27°47.220'N 126°53.922'E), off Okinawa Island, East China Sea, 976 m

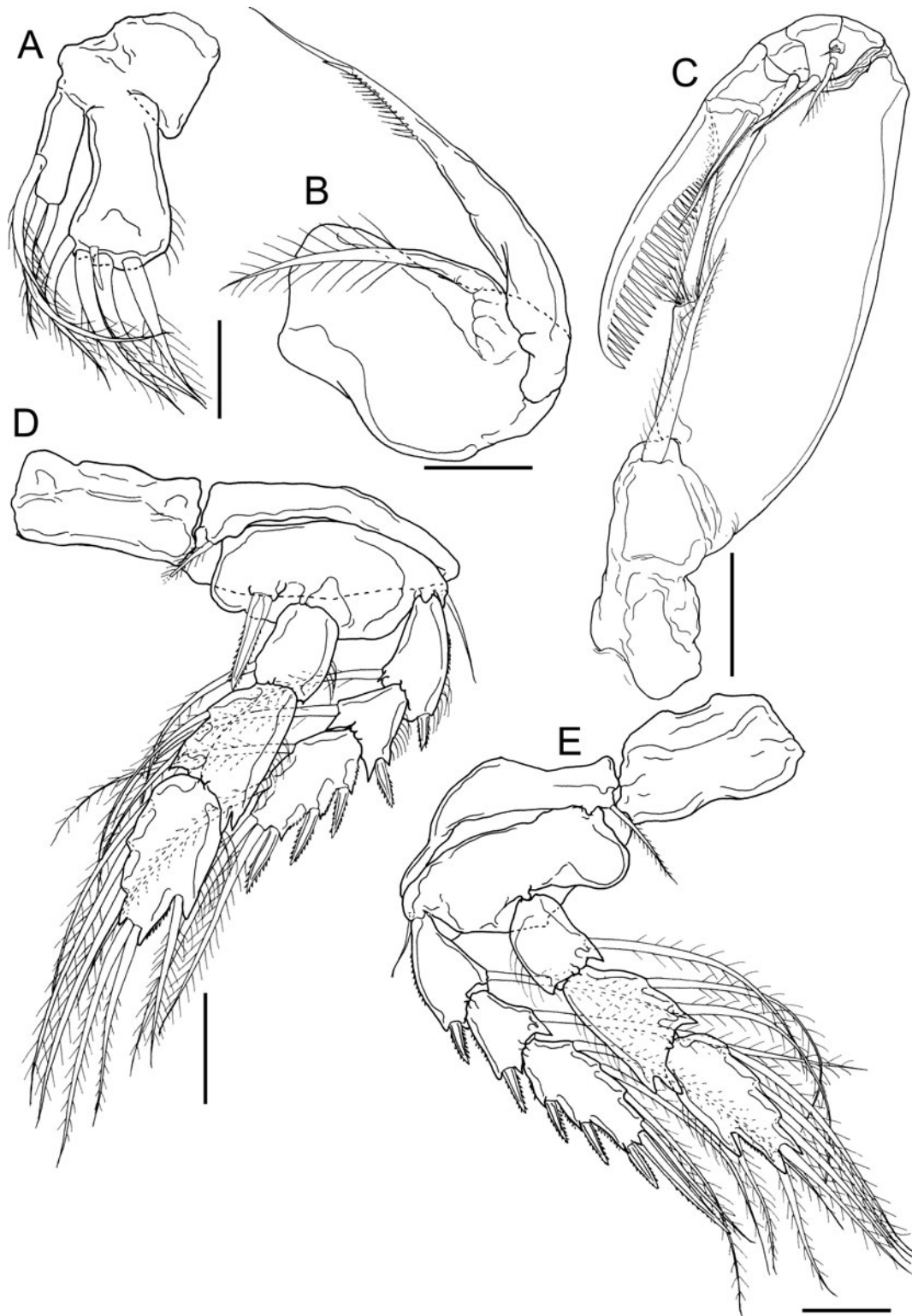


Fig. 3. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, adult female (NSMT-Cr 28363). A, left maxillule, posterior; B, left maxilla, posterior; C, left maxilliped, posterior; D, left leg 1, anterior; E, right leg 2, anterior. Scale bars: A, B, 20 μ m; C, 40 μ m; D, E, 50 μ m.

depth, 26 September 1997; four nauplius I hatched from eggs (NSMT-Cr 28374), collection data same as that of NSMT-Cr 28363; one copepodid IV (NSMT-Cr 28375), collection data same as that of NSMT-Cr 28363.

Description

Adult female: body cycloform (Figure 2A) 970–1229 (1082 ± 66) long, composed of cephalothorax, second to fifth pedigerous

somites, genital double somite, and 3-segmented abdomen ($N = 11$). Cephalothorax (Figure 2A) wider than long, 441–498 (466 ± 16) \times 486–537 (509 ± 14), bearing pair of posterolateral pointed processes. Second to fourth pedigerous somites gradually narrower posteriorly. Prosome 647–767 (691 ± 33) long. Genital double somite (Figure 2A, B) slightly wider than long, 132–177 (149 ± 13) \times 153–174 (160 ± 6). Abdomen (Figure 2A, B) composed of three free somites, 57–87 (69 ± 9) \times 75–85 (80 ± 3), 48–67 (58 ± 9) \times

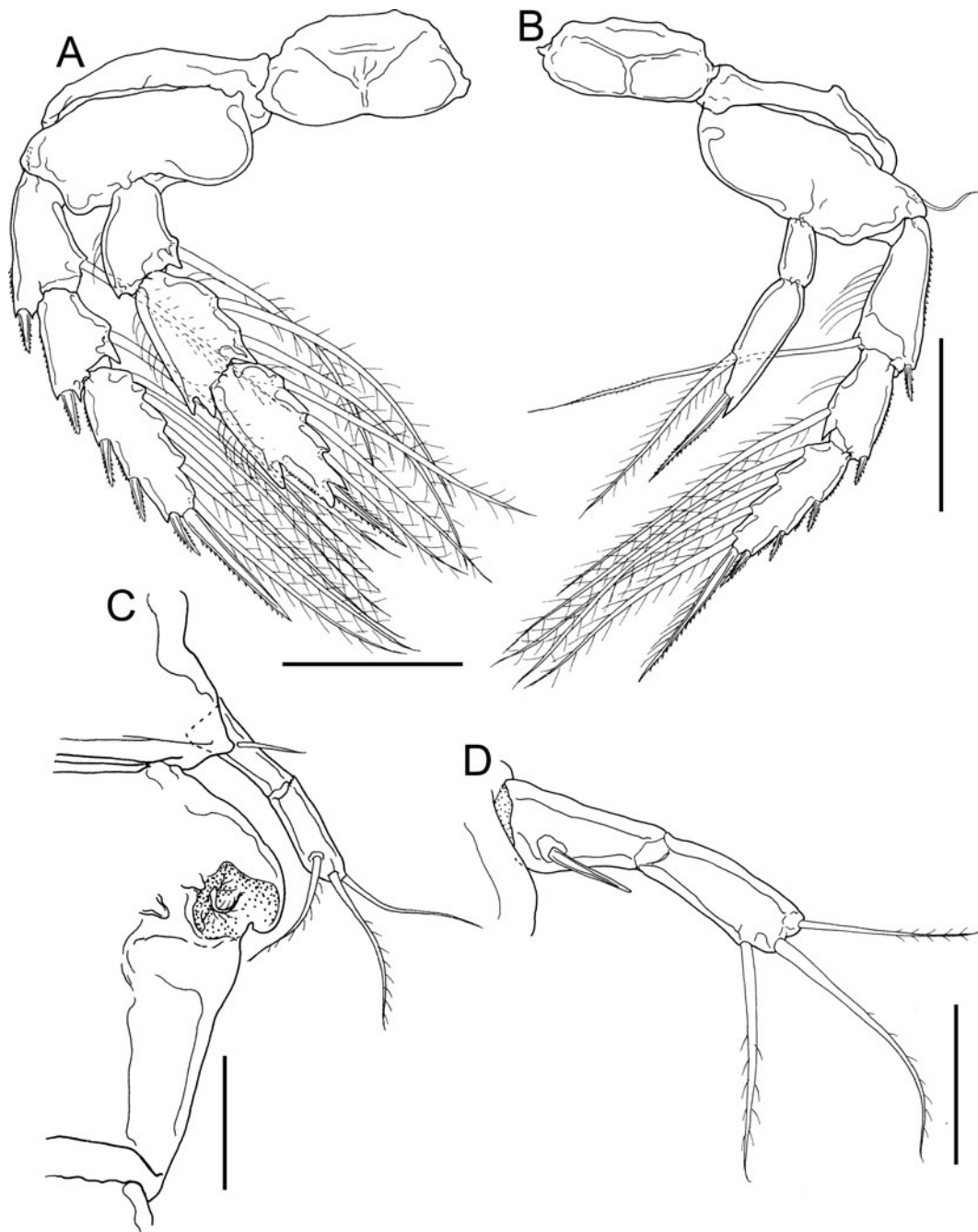


Fig. 4. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, adult female (NSMT-Cr 28363). A, right leg 3, anterior; B, left leg 4, anterior; C, partial view of fifth pedigerous somite and genital double somite, dorsal; D, right leg 5, dorsal. Scale bars: A, B, 100 μ m; C, 50 μ m; D, 40 μ m.

71–77 (74 ± 2) and 45–66 (55 ± 8) \times 60–73 (67 ± 4), respectively. Caudal rami (Figure 2A–C) 3.58–4.31 (3.97 ± 0.24) times longer than wide, 88–120 (102 ± 8) \times 24–29 (26 ± 2), with six setae on distal tip. Egg sac (Figure 2D) containing two eggs.

Rostrum (Figure 2E) bearing round margin. Antennule (Figure 2F) 10-segmented; armature formula 14, 9, 2, 4, 2, 2, 2, 2 + 1 aesthetasc, and 14; all setae naked. Antenna (Figure 2G) biramous, composed of coxa, basis, endopod, and exopod; coxa unarmed; basis ornamented with rows of marginal hairs; endopod 2-segmented, bearing one subterminal and three terminal setae on distal segment; exopod unsegmented, bearing one subterminal and one distal setae. Labrum (Figure 2H) shield shaped with median process. Mandible (Figure 2I) slender, bearing 10 distal teeth. Maxillule (Figure 3A) bilobed: large inner lobe (endite) with five setae and small outer lobe (palp) with three setae,

respectively. Maxilla (Figure 3B) composed of syncoxa and claw; syncoxa robust bearing long inner seta near articulation with claw; claw elongate bearing long pointed subterminal element and sharp tip. Maxilliped (Figure 3C) subchelate, comprising syncoxa, basis and 3-segmented endopod; syncoxa and basis bearing single inner seta, respectively; proximal endopodal segment bearing two tiny and single normal setae; middle segment of endopod bearing single seta; distal endopodal segment bearing single seta and pectinate claw with row of well-developed sharp processes on inner margin.

Legs 1 to 4 (Figures 3D, E & 4A, B) biramous; both rami 3-segmented, except 2-segmented endopod of leg 4. Leg armature formula shown in Table 1. Intercoxal sclerites of legs 1 to 4 (Figures 3D, E & 4A, B) unornamented. All spines serrated. All setae on rami plumose, except one seta with short marginal hairs on

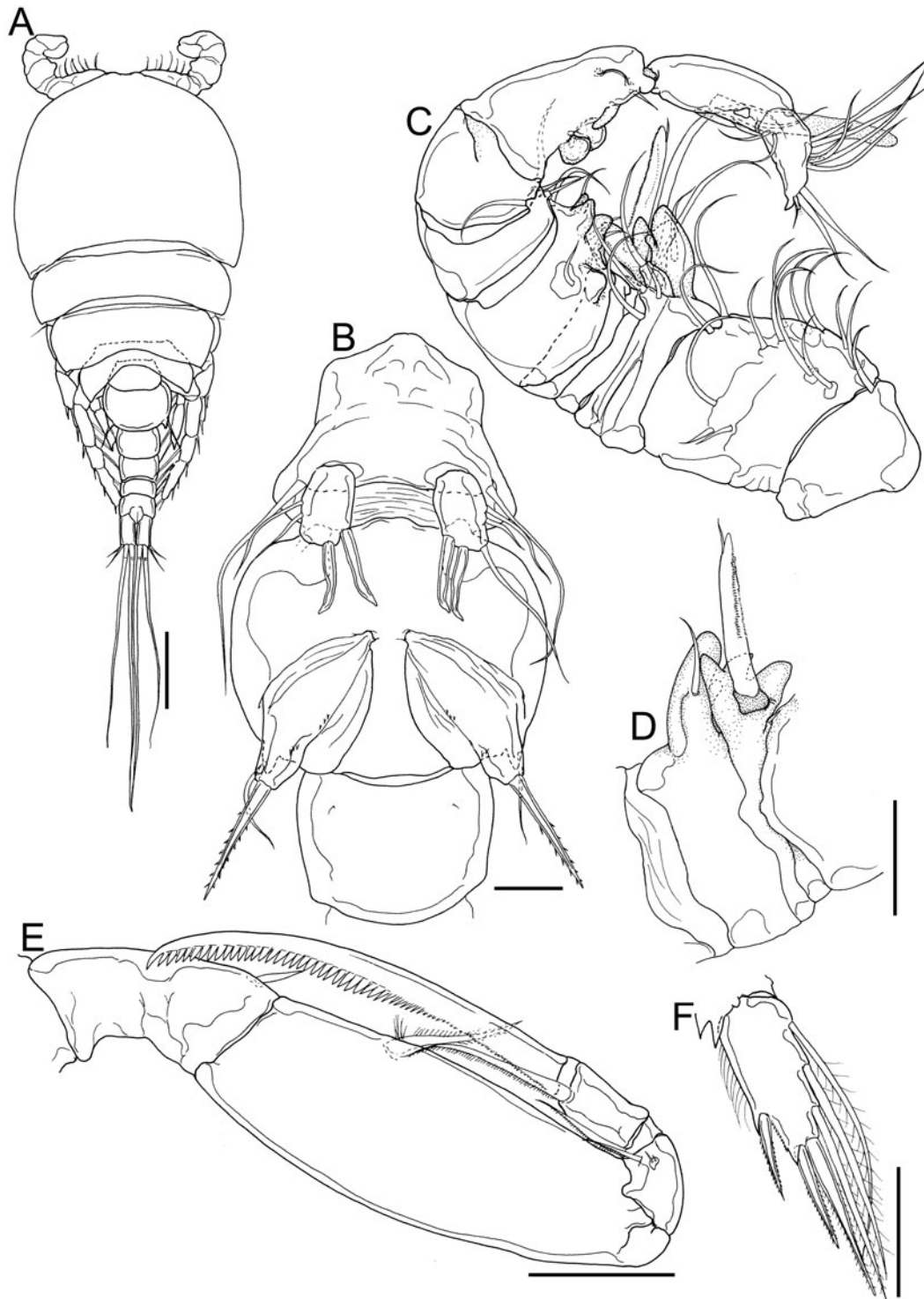


Fig. 5. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, adult male (NSMT-Cr 28364). A, habitus, dorsal; B, anterior part of urosome, ventral; C, right antennule, posterior; D, second to fifth segments of right antennule, anterior; E, right maxilliped, posterior; F, right third endopodal segment of leg 2, anterior. Scale bars: A, 100 μ m; B, D, 20 μ m; C, E, 30 μ m; F, 50 μ m.

proximal endopodal segment of leg 4. Rami of legs 1 to 4 bearing pointed processes on outer, inner and distal margins. Leg 5 (Figure 4C, D) 2-segmented; proximal segment bearing 1 basal naked element; distal segment bearing three distal plumose setae. Leg 6 (Figure 4C) represented by single small element at genital opening.

Adult male: body (Figure 5A) cyclopiform, 590–652 (627 \pm 22) long, composed of cephalothorax, second to fifth pedigerous somites, genital somite and 4-segmented abdomen (N = 10).

Cephalothorax wider than long, 248–263 (256 \pm 5) \times 290–310 (302 \pm 7), bearing pair of posterolateral pointed processes. Prosome 386–422 (406 \pm 12) long. Genital somite (Figure 5A, B) wider than long, 63–78 (71 \pm 6) \times 85–90 (88 \pm 2). Abdomen (Figure 5A) composed of four free somites, 35–50 (41 \pm 5) \times 49–57 (53 \pm 2), 29–41 (36 \pm 4) \times 46–52 (49 \pm 2), 28–41 (32 \pm 6) \times 41–46 (43 \pm 2) and 28–43 (32 \pm 6) \times 39–48 (42 \pm 2), respectively. Caudal rami (Figure 5A) 2.16–2.79 (2.50 \pm 0.21) times longer than wide, 32–44 (38 \pm 4) \times 14–19 (15 \pm 2), with six setae on distal tip.

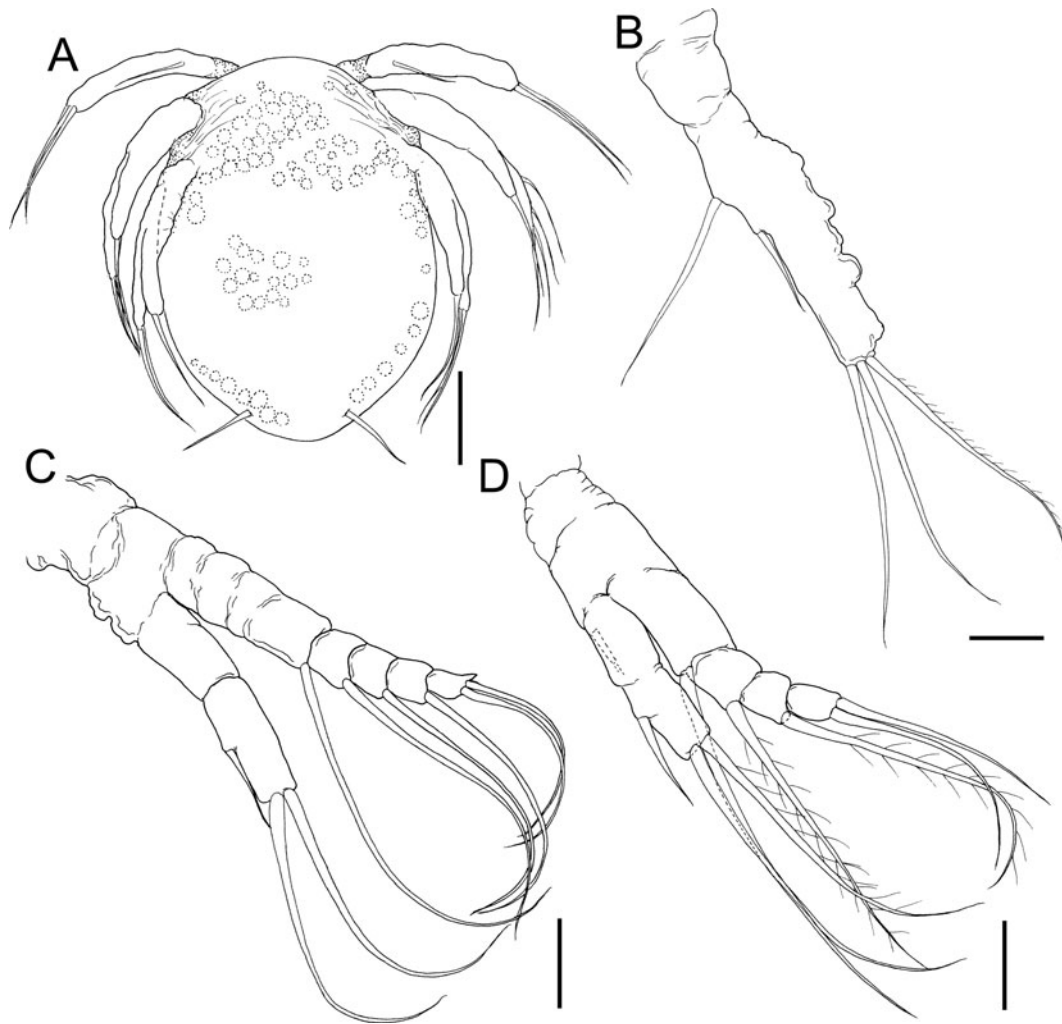


Fig. 6. *Stygiopontius senckenbergii* Ivanenko & Ferrari, 2013, nauplius I (NSMT-Cr 28374). A, habitus, ventral; B, left antennule, anterior; C, left antenna, anterior; D, left mandible, anterior. Scale bars: A, 100 μ m; B–D, 40 μ m.

Antennule (Figure 5C, D) 11-segmented, geniculated between ninth and tenth segments; armature formula 1, 14, 7, 2, 2, 4, 2, 2, 4, 4 + 1 aesthetasc, and 12; all setae naked except one stout serrated seta on fourth segment (Figure 5D); third segment bearing digitiform process with accessory element; fourth and sixth segments each bearing three conical processes. Antenna, mandible, maxillule and maxilla as in female. Maxilliped (Figure 5E) as in female except terminal pectinate claw with row of processes less well developed than in female.

Armature formula of legs 1 to 4 as in female except third endopodal segment of leg 2: I, II, 1, 2 (Figure 5F). Leg 5 (Figure 5B) composed of protopod with outer seta incorporated in fifth pedigerous somite and exopod bearing three slender outer and two stout distal setae. Leg 6 (Figure 5B) represented by genital flap bearing serrated spine and seta on outer margin.

Nauplius I: body ovoid (Figure 6A), longer than wide, 198–206 (203 ± 4) \times 138–158 (148 ± 8) (N = 4), filled with yolk. Caudal rami represented by pair of slender setae (Figure 6A). Naupliar eye not observed. Mouth and anal opening absent. Antennule (Figure 6B) unsegmented, two setae on ventral margin and three setae on distal tip. Antenna (Figure 6C) biramous: coxa without masticatory process incompletely fused to unarmed basis; exopod 5-segmented bearing 1, 1, 1, 1 and 2 setae per segment; endopod 2-segmented bearing proximal segment unarmed and distal segment with one middle and two distal setae. Mandible (Figure 6D) biramous: unarmed coxa incompletely fused to unarmed basis; exopod 4-segmented bearing 1, 1, 1

and 2 setae per segment; endopod unsegmented bearing two inner setae and two distal setae.

Copepodid IV: body cyclopidiform (Figure 7A) 646 long (N = 1), composed of 4-segmented prosome (cephalothorax, second to fourth pedigerous somites) and 4-segmented urosome (one pedigerous, genital and two abdominal somites). Cephalothorax (Figure 7A) wider than long, 301 \times 328. Prosome 445 long. Urosome 221 long. Caudal rami (Figure 7A–C) 2.31 times longer than wide, 46 \times 20, with one subdistal and five distal setae.

Antennule (Figure 7D) 10-segmented; armature formula 9, 5, 2, 4, 2, 2, 2, 2, 2 + 1 aesthetasc, and 14; all setae naked. Antenna, mandible, maxillule, and maxilla as in adult female. Maxilliped (Figure 7E) subchelate, comprising syncoxa, basis, and 2-segmented endopod; syncoxa and basis each bearing single inner seta; proximal endopodal segment bearing normal seta; distal endopodal segment bearing single seta and pectinate claw with row of well-developed sharp processes on inner margin.

Legs 1 to 4 (Figure 8A–D) biramous; both rami 2-segmented. Leg armature formula shown in Table 2. Leg 5 (Figures 7B & 8E) unsegmented bearing one basal naked element and three distal elements. Leg 6 (Figure 8E) represented by single element on lateral lobe.

Remarks

Based on both sexes, *Stygiopontius senckenbergii* belongs to a group characterized by leg 1 with an inner coxal seta and leg 4

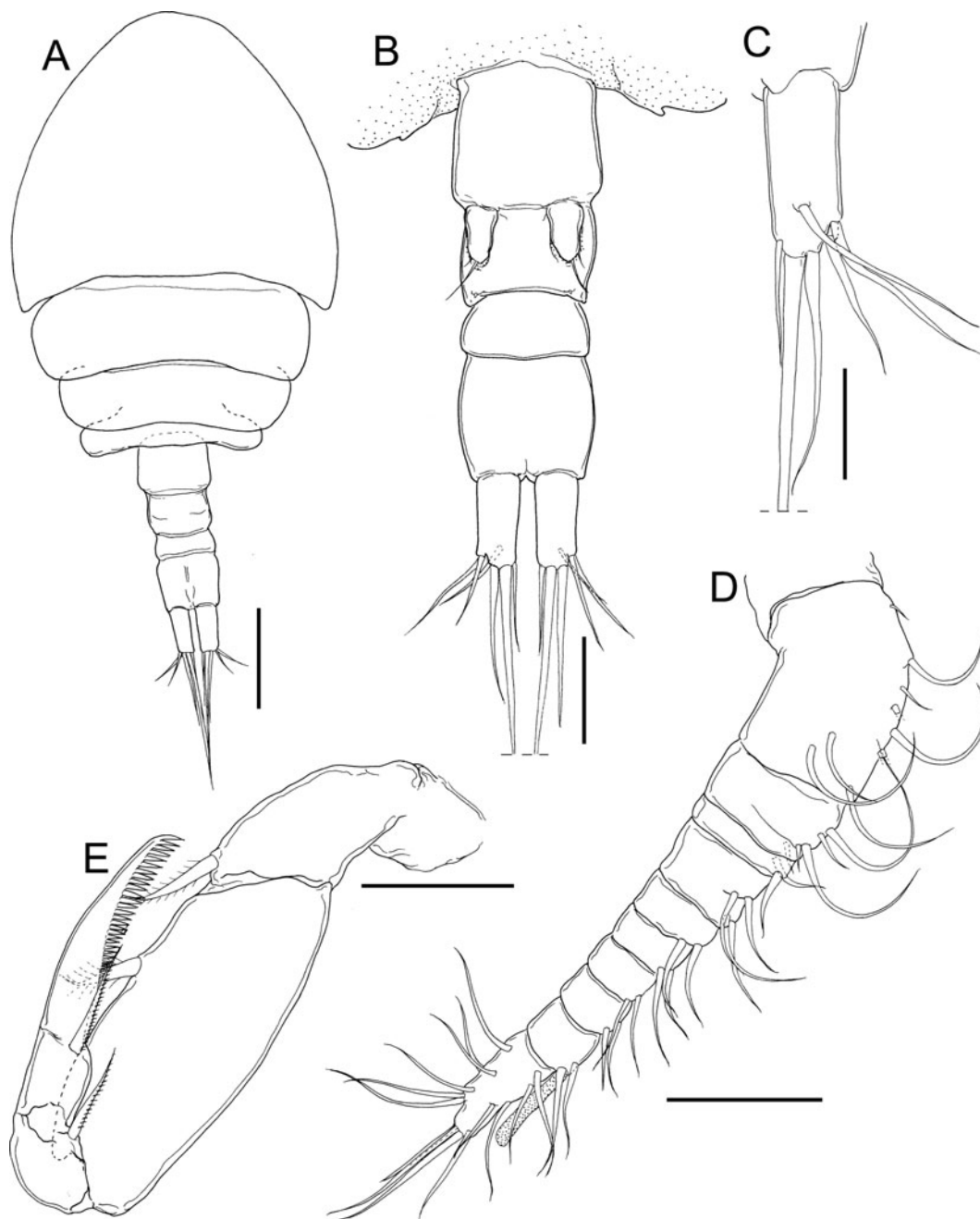


Fig. 7. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, copepodid IV (NSMT-Cr 28375). A, habitus, dorsal; B, urosome, ventral; C, right caudal ramus, dorsal; D, right antennule, anterior; E, left maxilliped, posterior. Scale bars: A, 100 μm ; B, 50 μm ; C, 30 μm ; D, E, 40 μm .

with four spines on the distal exopodal segment which comprises the following eight congeners: *S. brevispina*, *S. flexus* Humes, 1987, *S. hispidulus* Humes, 1987, *S. lauensis*, *S. mirus* Humes, 1996, *S. pectinatus*, *S. senckenbergi* and *S. sentifer* Humes, 1987 (Ivanenko & Ferrari, 2013). Among those congeners, four species (*S. brevispina*, *S. hispidulus*, *S. lauensis* and *S. pectinatus*) share the same armature formula on legs 1 to 4 with *S. senckenbergi* but clearly differ by lack of a pointed conical distal process on the leg 4 endopod.

One of the examined males was found in mate guarding, with its antennules grasping onto the second urosomite of a copepodid IV female (Figure 9).

Newly established Japanese name: 'Ohmu-kudakuchi-mijinko' for the species. 'Ohmu' is the symbolic creature in Japan's leading fantasy animation movie. The multiple blue dots distributed on the copepod's body are reminiscent of the eyes in the normal condition of 'Ohmu'.

Genus *Dirivultus* Humes & Dojiri, 1981

Dirivultus kaiko sp. nov.

(Figures 11, 10–13)

Type Material

Holotype: adult female (NSMT-Cr 28376), ex *Lamellibrachia columna* Southward, 1991 (Annelida: Siboglinidae), the Iheya North Knoll (27°47.371'N 126°53.843'E), off Okinawa Island, East China Sea, 987 m depth, 16 November 2018.

Allotype: adult male (NSMT-Cr 28377), collection data same as that of holotype.

Paratypes: 3 adult females and 2 adult males (NSMT-Cr 28378), collection data same as that of holotype.

Attachment Sites

The copepods inhabited the inner lamellar pockets in the tentacular crown of *L. columna* (Figure 1H, I).

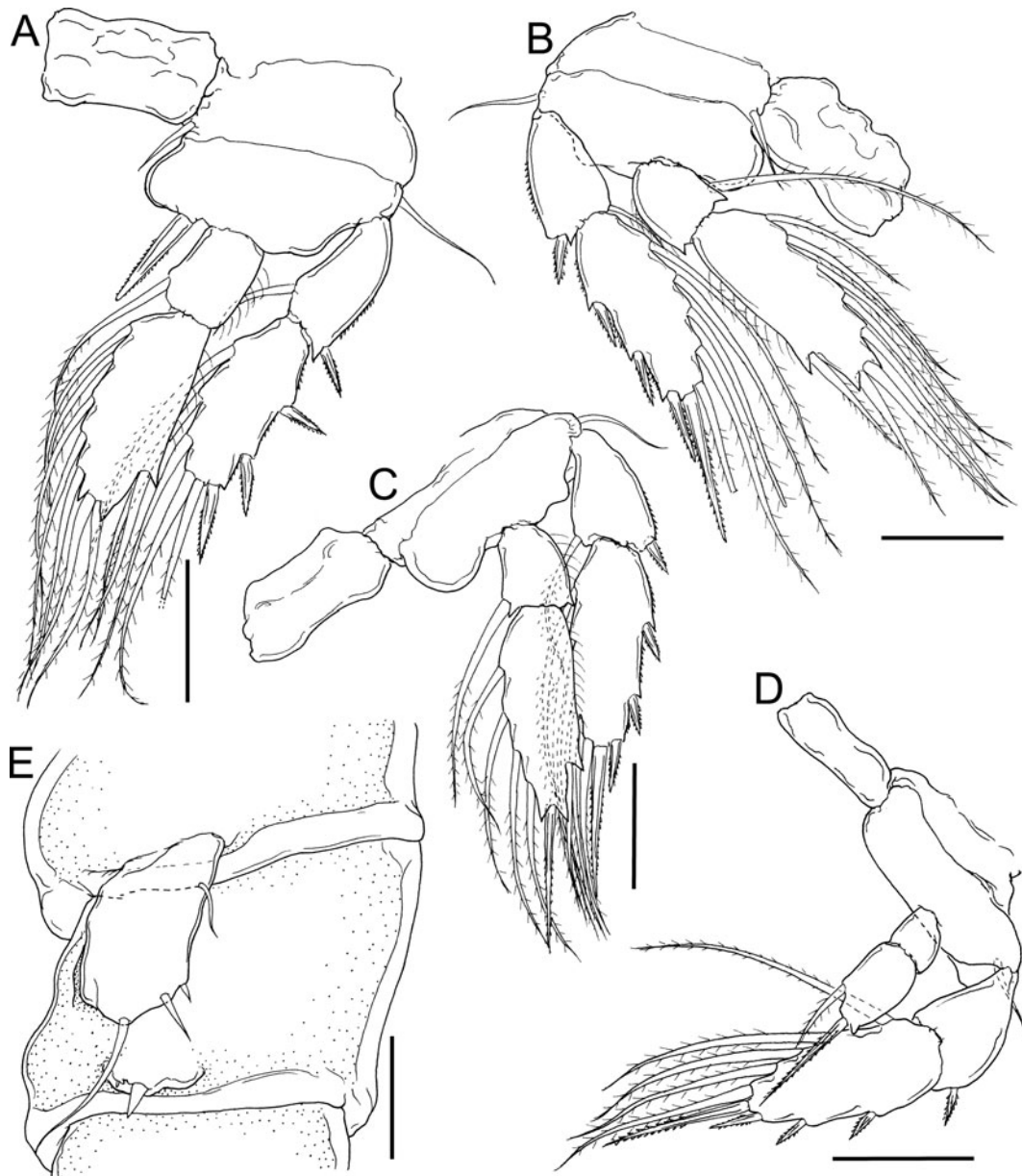


Fig. 8. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, copepodid IV (NSMT-Cr 28375). A, left leg 1, anterior; B, right leg 2, anterior; C, left leg 3, anterior; D, left leg 4, anterior; E, anterior part of urosomites. Scale bars: A–D, 50 μ m; E, 20 μ m.

Etymology

The species name 'kaiko' refers to the ROV 'Kaiko 7000II'.

Description

Holotype adult female: body cyclopiform (Figure 10A) 1240 long, composed of cephalothorax, second to fifth pedigerous somites, genital double somite and 3-segmented abdomen. Cephalothorax (Figure 10A) wider than long, 434 \times 554. Second to fourth pedigerous somites gradually narrower posteriorly. Prosome 822 long. Genital double somite (Figure 10A, B) distinctly wider than long, 154 \times 256; paired genital openings situated on dorsal surface (Figure 10C). Abdomen (Figure 10A, B) composed of three free somites, 75 \times 127, 89 \times 123 and 90 \times 115, respectively. Caudal rami (Figure 10A, B, D) 1.95 times longer than wide, 91 \times 47, with six setae on distal tip. Egg sac multiseriate (Figure 10A).

Rostrum (Figure 10E, H) bearing round margin without distinct apex. Antennule (Figure 10F) 13-segmented; armature formula 1, 12, 4, 1, 2, 1, 2, 1, 2, 2, 1, 1 + 1 aesthetasc, and 12; all setae naked; second segment bearing long recurved process

directed posteromedially (Figure 10E, F). Antenna (Figure 10G) biramous, composed of coxa, basis, endopod, and exopod; coxa unarmed; basis armed with row of marginal hairs; endopod 2-segmented, bearing spinules on proximal segment and one subterminal and three terminal setae on distal segment; exopod unsegmented, bearing two distal setae.

Labrum forming oral cone with labium (Figure 10H). Oral cone with two dentiform processes on posterior part of base.

Mandible (Figure 10I) slender, bearing fine distal teeth. Maxillule (Figure 11A) bilobed: large inner lobe (endite) with four long and one short distal setae and small outer lobe (palp) with one subterminal and two distal setae. Maxilla (Figure 11B) 2-segmented; syncoxa robust, unarmed; second segment covered with fine setules with elongate claw-like spine. Maxilliped (Figure 11C) subchelate, comprising syncoxa, basis and 2-segmented endopod; syncoxa incompletely incorporated to basis, bearing one seta and three pointed processes; basis bearing two processes; proximal endopodal segment bearing one seta, one small spiniform element and one process; distal endopodal segment bearing one spine-

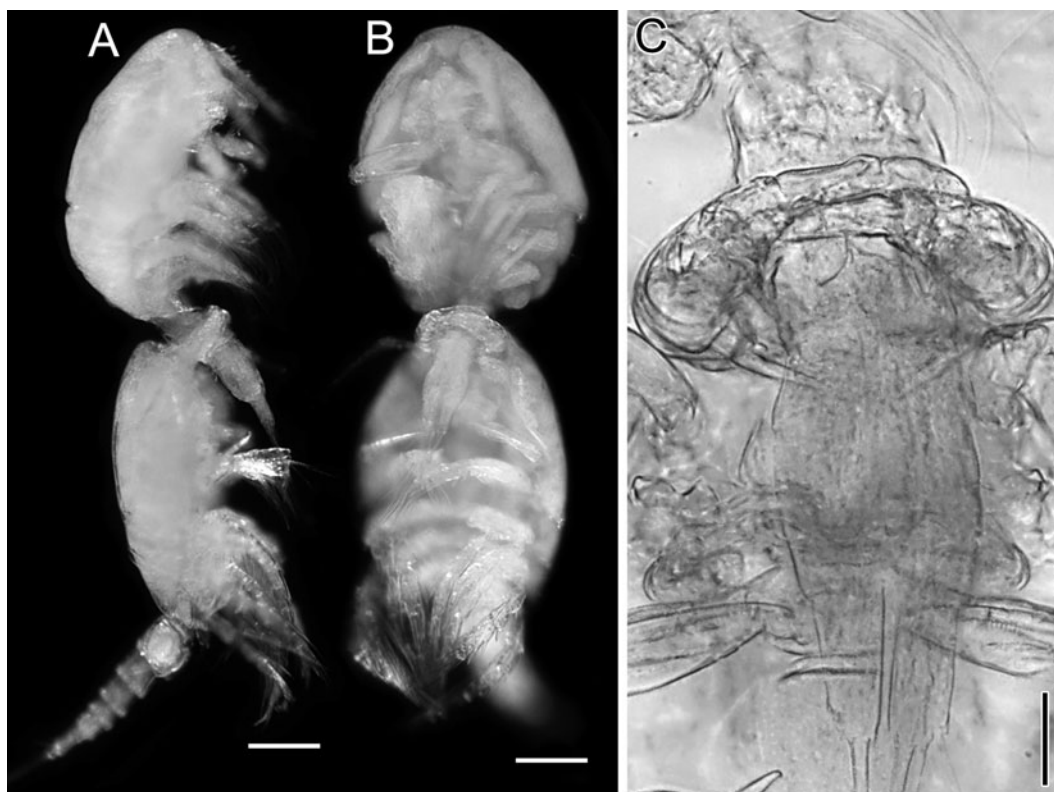


Fig. 9. *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, mating pair, showing adult male grasping urosomite of copepodid IV. A, lateral view of mating pair; B, same, ventral view; C, urosomite of copepodid IV grasped by antennules of male. Scale bars: A, B, 100 μ m; C, 30 μ m.

Table 1. Armature formula of legs 1 to 4 of *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, adult female. Arabic numbers = number of setae, Roman numbers = number of spines

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 3
Leg 2	0-1	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 3
Leg 4	0-0	1-0	I-1; I-1; III, I, 4	0-0; I, 1

Table 2. Armature formula of legs 1 to 4 of *Stygiopontius senckenbergi* Ivanenko & Ferrari, 2013, copepodid IV. Arabic numbers = number of setae, Roman numbers = number of spines

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; II, I, 5	0-1; 1, 2, 5
Leg 2	0-1	1-0	I-1; III, I, 5	0-1; 1, 2, 5
Leg 3	0-0	1-0	I-1; III, I, 5	0-1; 1, I, 4
Leg 4	0-0	1-0	I-0; III, I, 5	0-0; I, 1

like seta and terminal claw with median protrusion on concave margin.

Legs 1 to 4 (Figures 11D, E & 12A, B) biramous; both rami 3-segmented, except endopod of leg 4. Leg armature formula shown in Table 3. Intercoxal sclerites of legs 1 to 4 (Figures 11D, E & 12A, B) unornamented. All spines serrated. All setae on rami plumose. Leg 5 (Figure 12C) represented by one minute element. Leg 6 not observed.

Allotype adult male: body (Figure 12D) cyclopiform, 1180 long, composed of cephalothorax, second to fifth pedigerous somites, genital somite, and 4-segmented abdomen. Cephalothorax wider than long, 400 \times 574. Prosome 694 long. Genital somite (Figures 12D, E & 13A) wider than long, 144 \times 217. Abdomen (Figure 12D, E) composed of four free somites, 109 \times 146, 90 \times 131, 81 \times 113, and 77 \times 109, respectively. Caudal rami (Figure 12D, E) 1.80 times longer than wide, 86 \times 48, with six setae on distal tip.

Antennule (Figure 13B-D) 12-segmented; armature formula 1, 12, 3, 4, 2, 2, 4, 2, 2, 2, 1 + 1 aesthetasc, and 12; all setae naked; second segment bearing long recurved process directed posteromedially (Figure 13D); third segment bearing bifid process on posterior margin (Figure 13C); fourth and fifth

segments bearing digitiform processes on posterior margins (Figure 13C); fifth segment bearing distal pointed corner. Antenna, mandible, maxillule, maxilla, and legs 1 to 4 as in female. Maxilliped as in female except syncoxa with two processes (i.e. lacking second small pointed process shown on female).

Leg 5 (Figure 13A) composed of protopod incorporated in fifth pedigerous somite with outer naked seta and unsegmented exopod bearing two spatulate terminal setae. Leg 6 (Figure 13A) represented by genital flap bearing blunt distal spine and outer naked seta.

Variability: morphology of the female paratypes as in the holotype. The measurements of the body parts (N = 3) are as follows: body length, 1071-1327 (1211 \pm 130); cephalothorax wider than long, 417-457 (432 \pm 22) \times 492-535 (515 \pm 22); prosome length, 772-898 (837 \pm 63); genital double somite wider than long, 117-165 (148 \pm 27) \times 242-247 (244 \pm 2); first and second urosomites and anal somite length and width as follows, 60-83 (71 \pm 12) \times 115-123 (117 \pm 5), 51-80 (67 \pm 15) \times 108-109 (109 \pm 0), and 79-103 (93 \pm 12) \times 92-105 (98 \pm 6); caudal ramus 2.18-2.33 (2.27 \pm 0.08) times longer than wide, 83-89 (86 \pm 3) \times 37-

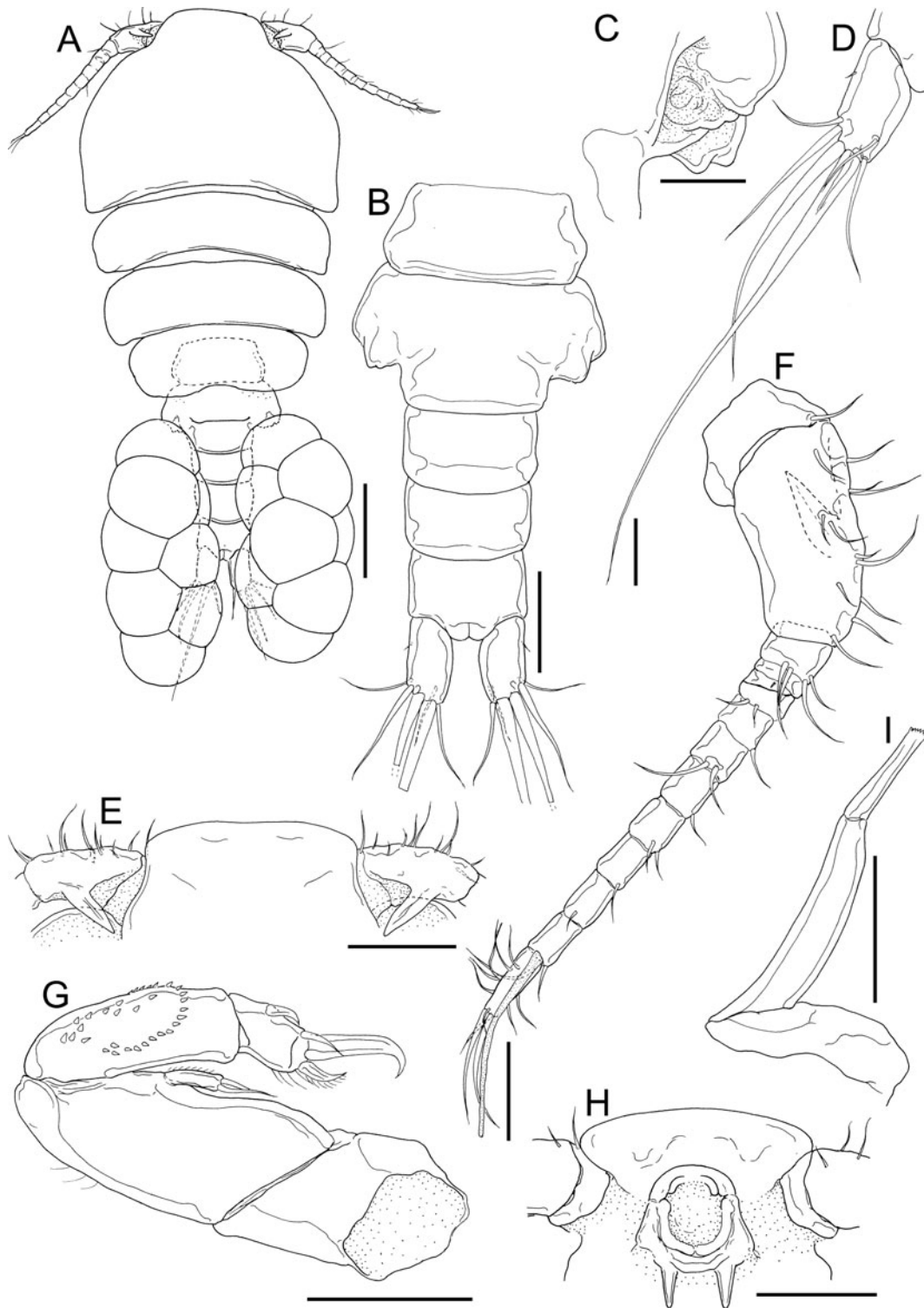


Fig. 10. *Dirivultus kaiko* sp. nov., adult female, holotype (NSMT-Cr 28376). A, habitus, dorsal; B, urosome, ventral; C, right genital aperture; D, left caudal ramus, dorsal; E, rostral area and basal part of antennules, dorsal; F, left antennule, posterior; G, left antenna; H, oral cone; I, right mandible, anterior. Scale bars: A, 200 μ m; B, E, H, 100 μ m; C, I, 40 μ m; D, F, G, 50 μ m.

39 (38 ± 1). Morphology of the male paratypes as in the allotype. The measurements of the body parts ($N = 2$) are as follows: body length, 1309–1320 (1314 ± 8); cephalothorax wider than long, 409–466 (438 ± 40) \times 586–597 (591 ± 8); prosome length, 757–802 (780 ± 32); genital somite wider than long, 148–159 (153 ± 8) \times 215–220 (218 ± 3); first to third urosomites and anal somite length and width as follows, 98–120 (109 ± 15) \times 150–154 (152 ± 3), 102–105 (103 ± 2) \times 122–131 (126 ± 7), 77–92 (85 ± 11) \times 113–114 (114 ± 0) and 83–91 (93 ± 12) \times 106–108 (107 ± 1);

caudal ramus 1.83–2.19 (2.01 ± 0.25) times longer than wide, 81–94 (88 ± 9) \times 43–44 (44 ± 1).

Remarks

So far, two congeners, *Dirivultus dentaneus* Humes & Dojiri, 1981 and *D. spinigulatus* Humes, 1999, were described based on both sexes (Humes & Dojiri, 1981; Humes, 1999). *Dirivultus kaiko* sp. nov. is clearly separated from those congeners by many characters (Table 4). In particular, antennules of

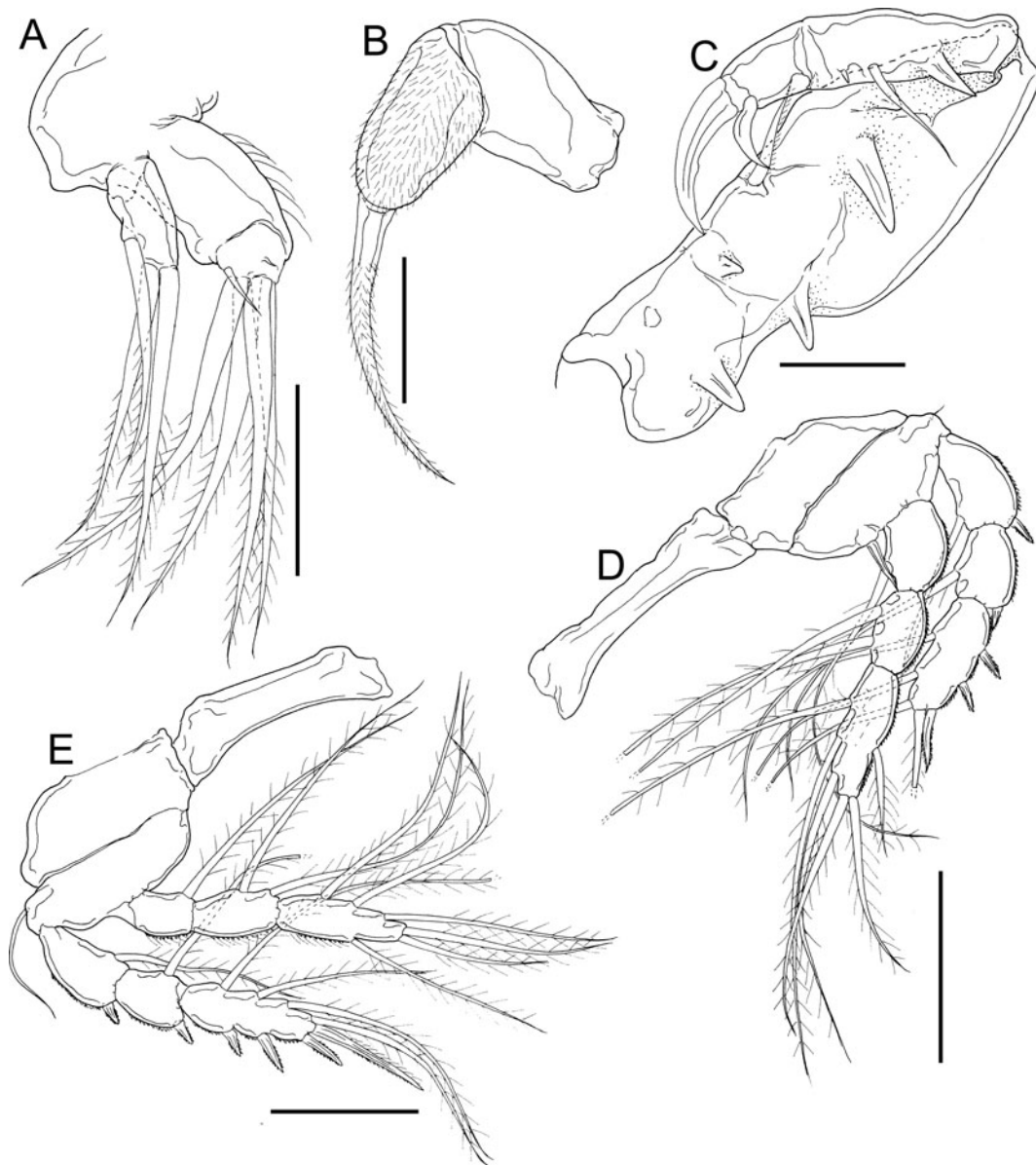


Fig. 11. *Dirivultus kaiko* sp. nov., adult female, holotype (NSMT-Cr 28376). A, right maxillule, anterior; B, left maxilla, anterior; C, left maxilliped, posterior; D, left leg 1, anterior; E, right leg 2, anterior. Scale bars: A, B, 40 μ m; C, 50 μ m; E, F, 100 μ m.

both sexes with large recurved process directed posteromedially on the second segment are useful, only the males of *D. dentaneus* share a similar process on the sixth segment. In addition, these three congeners can be distinguished even by egg sac: with uniseriate eggs on *D. spinigulatus*, single egg on *D. dentaneus* and multiseriate eggs on the new species.

Newly established Japanese name: 'Haori-kudakuchi-mijinko-zoku' and 'Haori-kudakuchi-mijinko' for the genus and species, respectively. Those names allude to the Japanese name of siboglinid tubeworms 'Haori-mushi'.

Discussion

Stygiopontius senckenbergi was originally described based on two adult males from the New Ireland Fore-Arc system, Papua New Guinea (Ivanenko & Ferrari, 2013). The present study represents the second record of the species as well as the first discovery of its adult female, nauplius I and copepodid IV. Now, both sexes have been described on 11 species of *Stygiopontius* (*S. brevispina*, *S. cladarus* Humes, 1996, *S. geminus* Lee, Kim & Kim, 2020,

S. horridus, *S. lauensis*, *S. quadripaxillifer* Lee, Kim & Kim, 2020, *S. quadrispinosus* Humes, 1987, *S. regius* Humes, 1996, *S. senckenbergi*, *S. senokuchiae* and *S. serratus* Humes, 1996) (Humes, 1987, 1991, 1996; Ivanenko et al., 2011; Uyeno et al., 2018; Lee et al., 2020; present study). In almost all of these congeners, sexual dimorphism is distinctly shown on the antennule and legs 2 and 5. Three or four setae on the outer margin of the third endopodal segment of leg 2 are replaced into spines in males, except in *S. horridus* and *S. regius*. *Stygiopontius horridus* shows minor differences in leg 1. In the female, leg 5 is elongate and situated laterally, and its proximal segment is distinctly separated from the pedigerous somite. That of the male is short, situated ventrally, and its proximal segment is incorporated to the pedigerous somite.

The male antennule of *Stygiopontius* is geniculated between the penultimate and antepenultimate segments. During precopulatory mate guarding, the male of *S. quadrispinosus* uses the antennule to grasp the anterior portion of the urosome of both adult and copepodid V females (Huys & Boxshall, 1991). In this study, the adult male of *S. senckenbergi* was attached

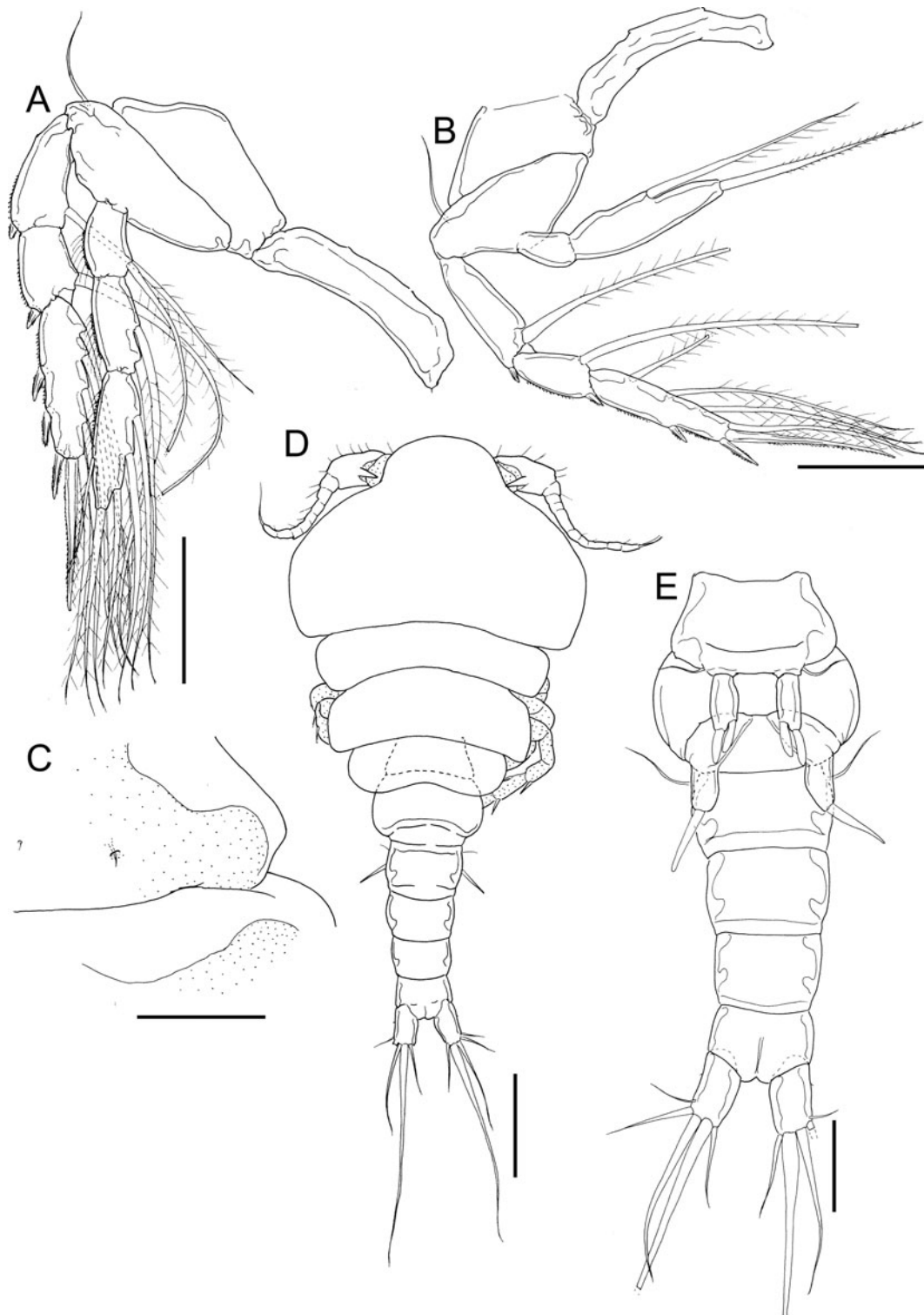


Fig. 12. *Dirivultus kaiko* sp. nov., A–C, adult female, holotype (NSMT-Cr 28376), and D, E, adult male, allotype (NSMT-Cr 28377). A, right leg 3, anterior; B, right leg 4, anterior; C, partial fifth pedigerous somite with left leg 5; D, habitus, dorsal; E, urosome, ventral. Scale bars: A, B, E, 100 µm; C, 40 µm; D, 200 µm.

on the second urosomite of the copepodid IV by the antennules (Figure 9A–C). A stout serrated seta on the fourth segment works to pinch the dorsal side of the abdomen of the copepodid.

The general body form and armature of the nauplius I of *S. senckenbergi* are similar to those of *S. pectinatus* (see Ivanenko *et al.*, 2007). As in *S. pectinatus*, the nauplius I of *S. senckenbergi* has characteristics typical of lethithotrophy, i.e. hairs are absent on the antennal coxa in the masticatory process and an oral

opening with a labrum is not observed. The antenna, mandible, maxillule and maxilla of the copepodid IV are basically similar to those of adults. The antennule is also similar to that of the adult female, but there are fewer setae on the proximal to third segments. In the order Siphonostomatoida, sexual dimorphisms are generally observed from copepodid V (see Ivanenko *et al.*, 2001; Ivanenko & Ferrari, 2003b), except in several taxa e.g. Pennellidae which shows sexual dimorphism from copepodid II or III (chalimus I or II) on the maxilliped (Schram, 1979;

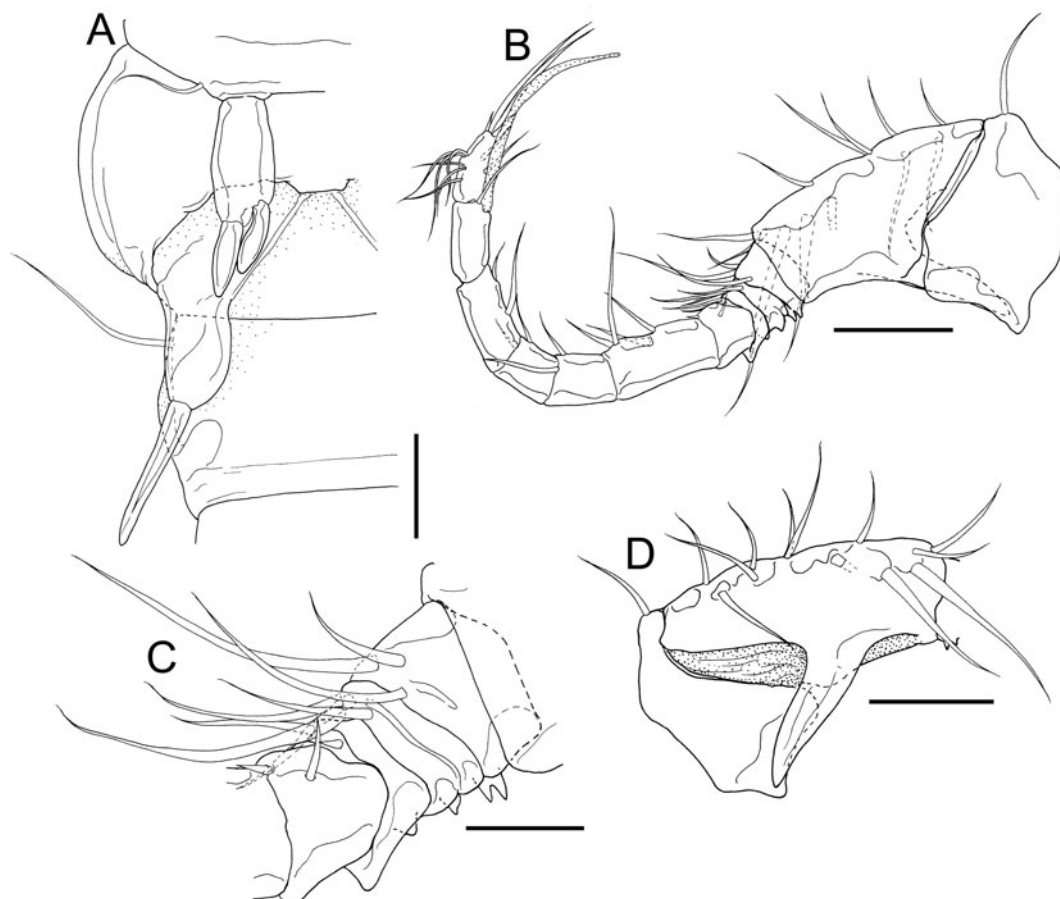


Fig. 13. *Dirivultus kaiko* sp. nov., adult male, allotype (NSMT-Cr 28377). A, right portion of anterior part of urosome; B, right antennule, posterior; C, third to sixth segments of right antennule, posterior; D, first and second segments of antennule, anterior. Scale bars: A, C, 20 μ m; B, D, 50 μ m.

Table 3. Armature formula of legs 1 to 4 of *Dirivultus kaiko* sp. nov., adult female. Arabic numbers = number of setae, Roman numbers = number of spines

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 3
Leg 2	0-0	1-0	I-1; I-1; III, I, 4	0-1; 0-2; 1, 2, 3
Leg 3	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, 1, 3
Leg 4	0-0	1-0	I-1; I-1; II, I, 4	0-0; I, 1

Perkins, 1983; Ismail *et al.*, 2013). Copepod IV is probably female, because adult males grasp individuals as is done in precopulatory mate guarding.

In this study, specimens of both sexes of *S. senckenbergi* were found on the ventral setae of the deep-sea squat lobster *Shinkaia crosnieri* which are covered with filamentous bacteria (Figure 1D, E). Although the instances of symbiosis by invertebrates are poorly known in hydrothermal vent fields, the members of the family Dirivultidae are associated with a variety of invertebrates (Boxshall & Halsey, 2004; Gollner *et al.*, 2010). Crustacean hosts including alvinocaridid shrimps, *Rimicaris* spp. and the bythograeid crab *Bythograea thermydron* Williams, 1980 have been reported (Humes, 1987, 1996; Humes & Lutz, 1994; Ivanenko *et al.*, 2006). *Stygiopontius senckenbergi* was originally described on the basis of specimens found without hosts in sediment samples collected by box-core from the New Ireland Fore-Arc system, Papua New Guinea (Ivanenko & Ferrari, 2013). *Shinkaia crosnieri* is distributed in hydrothermal vent fields off the Bismarck Archipelago, Papua New Guinea, close to the

type locality of *S. senckenbergi* mentioned above (Baba & Williams, 1998). The discovery of the host of *S. senckenbergi* in this study represents the first record of a dirivultid from *Shinkaia crosnieri*.

All three species of *Dirivultus* were found on the tentacular crowns of siboglinid tubeworms from the Pacific Ocean (*D. dentaneus* from *Lamellibrachia barhami* Webb, 1969 off southern California, eastern North Pacific; *D. spinigulatus* from an unidentified host close to *Escarpia* Jones, 1985 off Papua New Guinea, western South Pacific; and *D. kaiko* sp. nov. from *L. columna* in the Okinawa Trough, western North Pacific) (Humes & Dojiri, 1981; Humes, 1999; present study, Figure 1H, I). However, there are limited records of copepods associated with siboglinid tubeworms. Members of the family Dirivultidae have been found in wash residues from siboglinid tubeworms and associated invertebrates, except for species of *Chasmatopontius* Humes, 1980 and *Rimipontius* Humes, 1996 (e.g. Humes, 1987, 1989; Ivanenko & Ferrari, 2003a; Gollner *et al.*, 2010). Of those species found in association with siboglinid tubeworms, only three species of *Dirivultus*, as well as *Ceuthoecetes aliger* Humes & Dojiri, 1980, have been recorded from the tentacular crowns (Humes & Dojiri, 1980; Humes, 1987, 1999; present study). In other families, *Tychidion guyanense* Humes, 1973 (Cyclopoida: Erebonasteridae) was found from the same site as *Lamellibrachia luyesi* van der Land & Nørrevang, 1975 (= *Lamellibrachia* sp.) off Guyana, North Atlantic (Humes, 1973, 1984).

As a result of the present study, three species of the family Dirivultidae have now been recorded from Japanese waters since *S. senokuchiae* was reported from Izu-Bonin Arc (Uyeno *et al.*, 2018).

Table 4. Major distinguishing characters of adult stages of the three species of *Dirivultus* Humes & Dojiri, 1981 constructed after Humes & Dojiri (1981) and Humes (1999)

	<i>D. spinigulatus</i>	<i>D. dentaneus</i>	<i>D. kaiko</i> sp. nov.
Genital double somite (female)	With lateral lobes and dorsal ellipsoidal hyaline area	Without lateral lobes	With small lateral lobes
Genital somite (male)	Wider than long	Slightly longer than wide	Wider than long
Rostral spines	3 on female and 1 on male	Absent	Absent
Antennule (female)	2nd segment produced proximally on posterior margin as large spiniform process; distal corners of 7th to 10th segments pointed	With bifid processes on 5th to 9th segments and single process on 10th segment	2nd segment with large recurved process directed posteromedially
Antennule (male)	2nd segment swollen with lobe-like protrusion on anterior side; with 3 and 1 spines on 3rd and 4th segments, respectively	6th segment with large recurved process directed posteromedially; with 2 and 1 knobs on 5th and 6th segments, respectively; 1 bifid knob on 12th segment	2nd segment with large recurved process directed posteromedially; 3rd segment with bifid process; 4th and 5th segments with digitiform processes; distal corner of 5th segment pointed
Dentiform processes on oral cone	4	2	2
Area between insertions of maxillules	Without processes	Female with pair of stout processes	Without processes
Processes on maxilliped	4, 4, and 3 on first to third segments, respectively	6 on first segment on female and 4 on male	3, 2, and 1 on first to third segments on both sexes except 2 on first segment of male
Leg 1	3rd segment of exopod with II, II, 3; 1st and 2nd segments of endopod partly fused; intercoxal sclerite unarmed	3rd segment of exopod with II, I, 4; 1st and 2nd segments of endopod separated; intercoxal sclerite with pair of pointed processes	3rd segment of exopod with II, I, 4; 1st and 2nd segments of endopod separated; intercoxal sclerite unarmed
2nd endopodal segment of legs 2 and 3	With 1 inner seta	With 2 inner setae	With 2 inner setae
Leg 4	2nd segment of endopod with I, 1; intercoxal sclerite very short anteroposteriorly	2nd segment of endopod with I, 1; intercoxal sclerite unmodified	2nd segment of endopod with I, 1; intercoxal sclerite unmodified
Leg 5 (female)	Large process	Minute free segment with 1 seta	One minute element
Exopod of leg 5 (male)	With 1 outer and 2 spatulate terminal setae	With 2 broad terminal setae	With 2 spatulate terminal setae
Egg(s) in egg sac	Uniseriate	Single	Multiseriate

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