

Article



https://doi.org/10.11646/zootaxa.4415.2.8 http://zoobank.org/urn:lsid:zoobank.org:pub:AA0C8BA5-F4DC-4559-A26A-1F6BC133A0EA

A new dirivultid copepod (Siphonostomatoida) from hydrothermal vent fields of the Izu-Bonin Arc in the North Pacific Ocean

DAISUKE UYENO^{1,4}, HIROMI K WATANABE² & MOTOHIRO SHIMANAGA³

- ¹Graduate School of Science and Engineering, Kagoshima University, 1-21-35 Korimoto, Kagoshima 890-0065, Japan
- ²Japan Agency for Marine-Earth Science and Technology, Yokosuka, Kanagawa, Japan
- ³Kumamoto University, Kumamoto, Kumamoto, Japan
- ⁴Corresponding author. E-mail: duyeno@sci.kagoshima-u.ac.jp, Telephone and fax number: ++81-99-285-8167

Abstract

A new species of dirivultid copepod (Siphonostomatoida) is described from hydrothermal vents in a volcanic seamount in Izu-Bonin Arc, western part of North Pacific Ocean. The copepod was collected during the research cruise NT13-09 using the *R/V Natsushima* with the *ROV Hyper-Dolphin* in April 2013. The type series of the new species was collected from the populations of *Paralvinella* spp. (Annelida: Alvinellidae) on an active vent chimney at the depth of 795 m. *Stygiopontius senokuchiae* n. sp. is most closely related to *S. teres* Humes, 1996 but clearly distinguished from the latter species by the possession of the following characters: the basis of leg 1 with an attenuated inner process; the genital double somite with a conical process lateral to the genital opening; and caudal rami without distal process. The findings of the copepod in the present study represents the first record of nominal species of the Dirivultidae from Japanese waters and a record of the shallowest depth of the genus. A key to species of the genus *Stygiopontius* from Western Pacific is provided.

Key words: Dirivultidae, Ogasawara, Paralvinella spp., ROV Hyper-Dolphin, Stygiopontius senokuchiae n. sp.

Introduction

The family Dirivultidae Humes & Dojiri, 1981 (Copepoda: Siphonostomatoida) is known from hydrothermal vents, and some of its members have been found in the washings of polychaetes, gastropods, and bivalves (Boxshall & Halsey 2004). Among 13 genera of the family, *Stygiopontius* Humes, 1987 which contains 22 valid species is the largest genus, and all species were collected from hydrothermal vent communities in deep-sea of Pacific and Atlantic Oceans (Humes 1987, 1989, 1990, 1991, 1996, 1997; Ivanenko *et al.* 2006; Ivanenko & Ferrari 2013). According to Gollner et al. (2016), two undescribed species have recently been found from Central Indian Ridge, Indian Ocean. Records of many species are hitherto biased towards the Mid-Atlantic Ridge in the Atlantic Ocean and the East Pacific Rise and its neighbor and connecting ridges in the eastern part of the Pacific Ocean (Boxshall & Halsey 2004; Gollner *et al.* 2010). In western part of the Pacific Ocean, hence, only two species, *S. pectinatus* Humes, 1987 and *S. stabilitus* Humes, 1990, are known from Mariana Back-Arc Basin (Humes 1990). Although hydrothermal vent fields are located on plate boundaries and isolated from each other, it is reported that haplotype networks of intraspecific population connectivity of copepods between each vent is high based on analysis of partial nucleotide sequences of the mtCOI gene (Gollner *et al.* 2016). Studies of developmental stages of *Stygiopontius* are sparse but the morphology of nauplius I of *S. pectinatus* was revealed based on hatched specimens, and it is known to lecithotrophic (Ivanenko *et al.* 2007).

In this study, a new species of *Stygiopontius* is described based on specimens collected from the Izu-Bonin Arc.

Materials and methods

The field surveys were conducted during the cruise NT13-09 (April 2013) in calderas of three neighboring

seamounts in Izu-Bonin Arc, western part of North Pacific Ocean operated by the *R/V Natsushima* with the *ROV Hyper-Dolphin* belonging to Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Yokosuka, Japan. Copepods were sorted out from the sediment sampled close to hydrothermal vents (Fig. 1) with a suction sampler (Slurp Gun) lined with 32-µm mesh loaded on the ROV, fixed in 99% ethanol, and preserved for morphological study. Prior to the microscopic observation, selected specimens were soaked in lactophenol for 24 hours, dissected using sharpened tungsten needles under a stereomicroscope, and examined with the wooden slide method of Humes & Gooding (1964). Drawings were made with the aid of a compound microscope and a drawing tube. Body parts of copepods were measured using an ocular micrometer and are given in micrometers, 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).

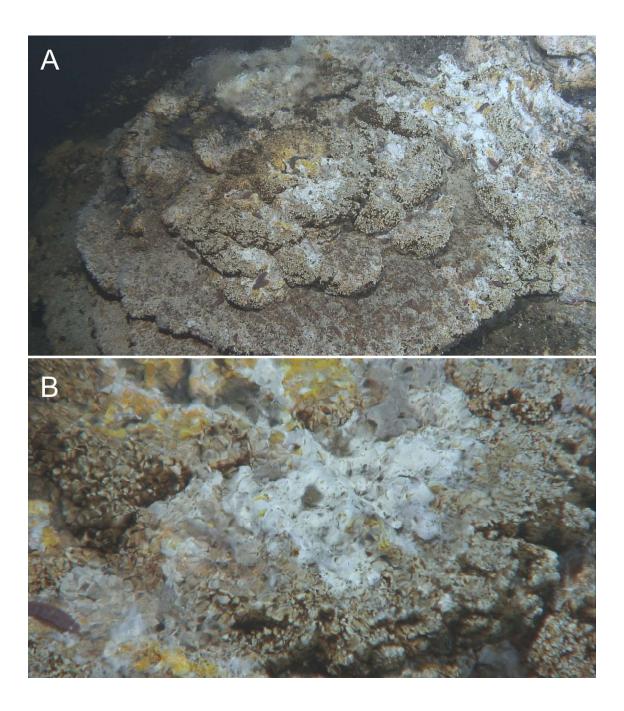


FIGURE 1. Sampling site of *Stygiopontius senokuchiae* **n. sp.** at 795 m depth on Myojin-sho Caldera, Izu-Bonin Arc. A, hydrothermal vents; B, magnified image of the site and populations of *Paralvinella* spp (yellowish portions) and bacterial mats (whitish portions).

Results

Stygiopontius senokuchiae n. sp. (Figs 2–4)

Type material. Holotype: adult female (NSMT-Cr 26842), ex populations of *Paralvinella* spp. (Polychaeta: Alvinellidae), Myojin-sho Caldera (31°53.042N, 139°58.220E), off northern Ogasawara Islands, North Pacific Ocean, depth 795 m, 24 April 2013. Allotype: adult male (NSMT-Cr 26843), collection data same as that of holotype. Paratypes: six adult females and five adult males (NSMT-Cr 26844), collection data same as that of holotype.

Description of holotype adult female. Body (Fig 2A) 792 long, cyclopiform composed of cephalothorax, second to fifth pedigerous somites, genital double somite, and 3-segmented abdomen. Cephalothorax wider than long, 391×455 , bearing pair of posterolateral pointed processes. Second to fourth pedigerous somites gradually narrower. Prosome 556 long. Genital double somite (Fig 2A, C) slightly longer than wide, 125×115 , bearing pair of conical, blunt process on lateral to genital openings and pair of pointed posterolateral processes. Abdomen (Fig 2A, C) progressively narrower posteriorly, composed of three free somites, 50×88 , 47×78 , and 47×71 , respectively. Caudal rami (Fig 2C, E) 1.31 times longer than wide, 36×27 , with six setae.

Rostrum (Fig 2B) bearing without distinct apex. Antennule (Fig 2F) 12-segmented; armature formula 1, 2, 12, 8, 2, 4, 2, 2, 2, 2, 2 + 1 aesthetasc, and 14; all setae naked, except single plumose seta on fifth segment. Antenna (Fig 2G) biramous, composed of coxa, basis, endopod, and exopod; coxa and basis unarmed; endopod 2-segmented, bearing single subterminal and three terminal setae; exopod unsegmented, bearing two setae. Oral cone (Fig 2B) ovoid. Mandible (Fig 2H) thin, slender, bearing row of spinules on subterminal part of inner margin and 10 distal teeth. Maxillule (Fig 2I) bilobed: large inner lobe (endite) and small outer lobe (palp) bearing four setae, respectively. Maxilla (Fig 2J) composed of syncoxa and claw; syncoxa robust bearing long seta near articulation with claw; claw elongate bearing spatulated and spinulated tip with spinules. Maxilliped (Fig 3A) subchelate, comprising syncoxa, basis, and 3-segmented endopod; syncoxa and basis bearing single seta, respectively; proximal endopodal segment bearing two tiny setae; middle segment of endopod bearing single seta; distal endopodal segment bearing single seta and claw with row of fine spinules on inner margin.

Legs 1 to 4 (Fig 3B–E) biramous; both rami bearing 3-segmented rami, except endopod of leg 4. Leg armature formula as follows:

	Coxa	Basis	Exopod	Endopod	
Leg 1	0-1	1-1	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; II, I, 4	0-0; I, 1	

Intercoxal sclerites of legs 1 to 4 (Fig 3B–E) unornamented. All spines spatulate, bearing serrated margins. All setae plumose. Leg 1 with basis bearing conical inner distal process. Leg 2 with row of setules on inner side of basis. Legs 3 and 4 with rounded protrusion between rami. Rami of legs 1 to 4 bearing pointed processes on outer and distal margins. Leg 5 (Fig 3F) indistinctly 2-segmented; proximal segment bearing 1 seta; distal segment bearing three distal setae; all of these 4 setae plumose. Leg 6 (Fig 2D) represented by single small seta at genital opening.

Description of allotype adult male. Body (Fig 4A) cyclopiform, 471 long, composed of cephalothorax, second to fifth pedigerous somites, genital somite, and 4-segmented abdomen. Cephalothorax wider than long, 187×257 , bearing pair of posterolateral pointed processes. Prosome 320 long. Genital somite (Fig 4A, B) wider than long, 45×76 . Abdomen (Fig 4A) progressively narrower posteriorly, composed of four free somites, 34×59 , 40×55 , 47, and 47×47 , respectively. Caudal rami (Fig. 4A) 1.41 times longer than wide, 47×47 , with six setae.

Antennule (Fig 4C) 11-segmented; armature formula 1, 2, 12, 6, 6, 4, 2, 2, 4, 4 + 1 aesthetasc, and 12; all setae naked. Antenna, mandible, maxillule, and maxilla as in female. Proximal endopodal segment of maxilliped (Fig 4D) bearing two setae.

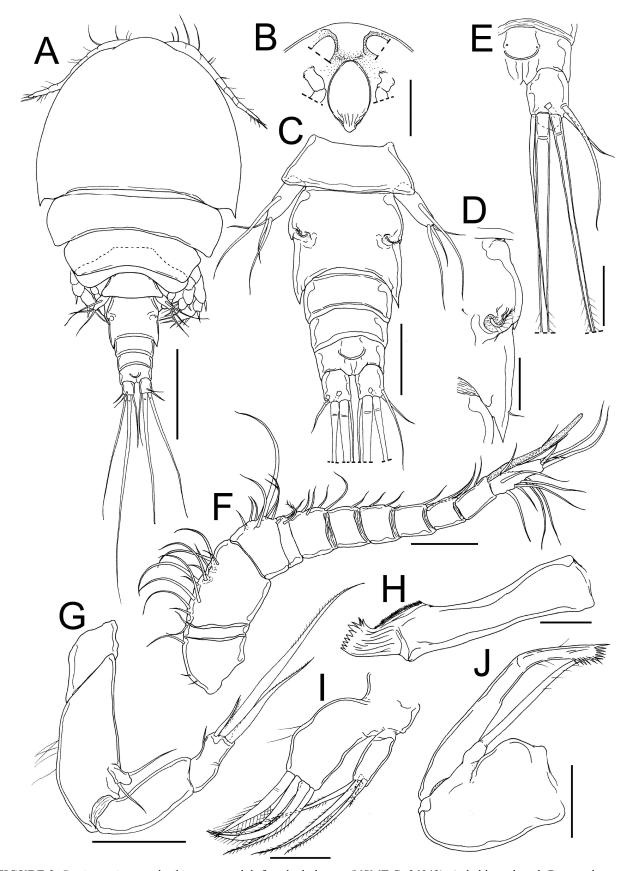


FIGURE 2. Stygiopontius senokuchiae **n.** sp. adult female, holotype (NSMT-Cr 26842). A, habitus, dorsal; B, rostral area; C, urosome, dorsal; D, genital aperture and leg 6, dorsal; E, right caudal ramus, dorsal; F, left antennule, posterior; G, right antenna, anterior; H, right mandible; I, right maxillule, posterior; J, right maxilla, posterior. Scale bars: A, 200 μ m; B, 100 μ m; C, 70 μ m; D, I, J, 30 μ m; E–G, 40 μ m; H, 20 μ m.

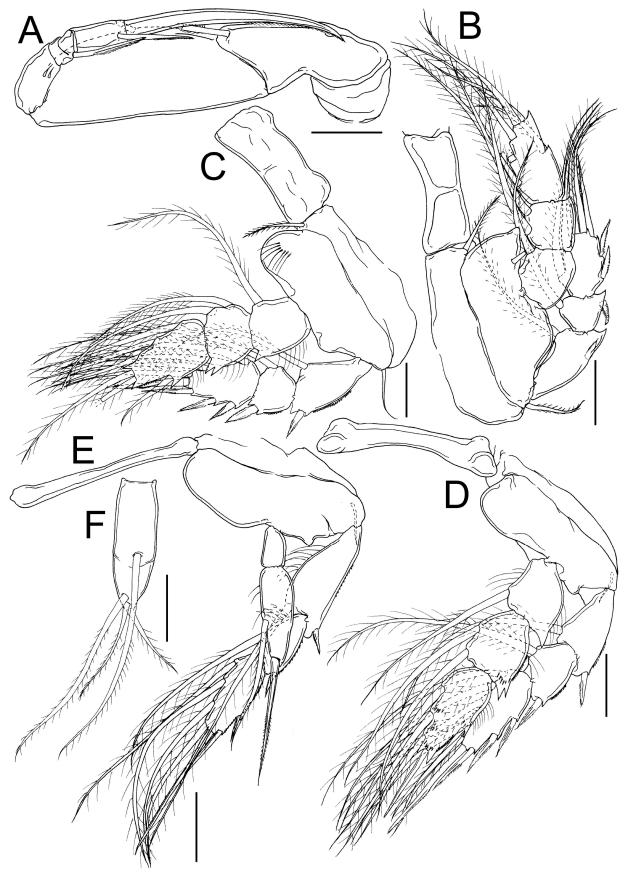


FIGURE 3. *Stygiopontius senokuchiae* **n. sp.** adult female, holotype (NSMT-Cr 26842). A, right maxilliped, posterior; B, right leg 1, anterior; C, left leg 2, anterior; D, left leg 3, anterior; E, left leg 4, anterior; F, right leg 5, dorsal. Scale bars: A, F, 30 μ m; B–E, 40 μ m.

Armature formula of legs 1 to 4 as in female. Armature formula of leg 2 as in female but single outer, two distal, and single inner plumose setae of third endopodal segment replaced into thick, spine-like setae. Leg 5 (Fig 4B) composed of protopod bearing 1 outer seta and exopod bearing three outer and two rod-shaped distal setae. Leg 6 (Fig 4B) represented by genital flap bearing single serrated spine and single seta on outer margin; posterior part of genital flap bearing row of spinules.

Variability. The morphology of the female paratypes as in the holotype. The measurements of the body parts (n = 6) are as follows: body length 685–786 (727 \pm 37); cephalothorax length 335–396 (365 \pm 26); cephalothorax width 387–431 (402 \pm 16); prosome length 484–538 (516 \pm 23); genital double somite length 94–123 (114 \pm 11); genital double somite width 107–126 (116 \pm 7); first urosomite length 51–63 (55 \pm 5); first urosomite width 78–88 (82 \pm 4); second urosomite length 40–55 (45 \pm 8); second urosomite width 73–80 (76 \pm 2); anal somite length 28–52 (38 \pm 8); anal somite width 65–69 (67 \pm 2); caudal ramus length 32–45 (39 \pm 5); caudal ramus width 25–29 (26 \pm 2). Caudal ramus 1.29–1.71 (1.48 \pm 0.15) times longer than wide.

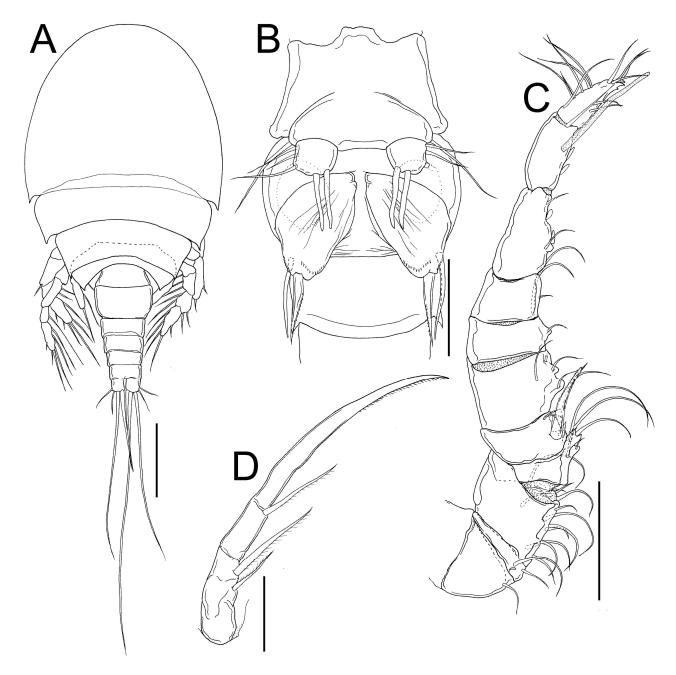


FIGURE 4. *Stygiopontius senokuchiae* **n. sp.** adult male, allotype (NSMT-Cr 26843). A, habitus, dorsal; B, fifth pedigerous somite to first urosomite, ventral; C, right antennule, posterior; D, endopod of right maxilliped, posterior. Scale bars: A, 100 μ m; B, 40 μ m; C, 30 μ m; D, 20 μ m.

The morphology of the male paratypes as in the allotype. The measurements of the male body parts of other material (n = 5) are as follows: body length 446–483 (464 \pm 15); cephalothorax length 208–258 (229 \pm 21); cephalothorax width 221–272 (251 \pm 19); prosome length 317–345 (331 \pm 13); genital somite length 48–56 (50 \pm 3); genital somite width 75–83 (78 \pm 3); first urosomite length 30–42 (37 \pm 4); first urosomite width 58–63 (59 \pm 2); second urosomite length 26–42 (34 \pm 6); second urosomite width 50–55 (52 \pm 2); third urosomite length 19–33 (26 \pm 6); third urosomite width 44–48 (47 \pm 2); anal somite length 18–26 (22 \pm 3); anal somite width 42–49 (44 \pm 3); caudal ramus length 24–26 (25 \pm 1); caudal ramus width 17–20 (18 \pm 2). Caudal ramus 1.22–1.45 (1.38 \pm 0.09) times longer than wide.

Remarks. So far 22 valid species are known in Stygiopontius. Seven species, S. cinctiger Humes, 1987, S. lomonosovi Ivanenko & Martínez Arbizu, 2006, S. mucroniferus Humes, 1987, S. rimivagus Humes, 1997, S. serratus Humes, 1996, S. teres Humes, 1996, and S. verruculatus Humes, 1987, share three spines and four setae on the third exopodal segment of the leg 4 with S. senokuchiae n. sp. (vs. other 15 species have four spines and four setae) (see Humes 1987, 1989, 1990, 1991, 1996; Ivanenko et al. 2006; Ivanenko & Ferrari 2013). Among the seven species, S. cinctiger, S. lomonosovi, and S. teres shares coxal setae both on legs 1 and 2 (see Humes 1987, 1996; Ivanenko & Martínez Arbizu, 2006). Stygiopontius cinctiger differs from the new species by having an inner spine on the basis of the leg 1 (vs. single inner seta) and the genital double somite without lateral and posterolateral processes (vs. with both lateral and posterolateral processes) (see Humes 1987). Stygiopontius lomonosovi is separated from the new species by having an inner seta on the bases of legs 3 and 4 (vs. no inner seta) (see Ivanenko & Martínez Arbizu 2006). Stygiopontius teres is similar to S. senokuchiae n. sp. but is distinguished from the new species by the following characters: the genital double somite has no lateral processes (vs. bearing a pair of conical processes); the caudal rami bears a pointed process on the posterodorsal margin (vs. without processes); the basis of leg 1 without inner distal processes (vs. bearing one conical inner distal process) (see Humes 1996). Further, on S. teres, the segmentation of the female antennule differs from that of the new species (the first segment appears indistinctly 3-segmented vs. distinctly 3-segmented) (see Humes 1996, fig. 16b).

Etymology. The specific name, *senokuchiae*, was chosen after Ms Reina Senokuchi who formerly studied copepods on hydrothermal fields in Izu-Bonin Arc and found the specimens of the new species.

Newly established Japanese name. "Rengoku-kudakuchi-mijinko-ka" for the family, "Rengoku-kudakuchi-mijinko-zoku" for the genus, and "Rengoku-kudakuchi-mijinko" for the species. In Japanese, the Purgatory is translated to "Rengoku", "kudakuchi" means a tube-like mouth of the copepod, and "mijinko" is a general term for tiny crustaceans.

Discussion

During the research cruise NT13-09 on Izu-Bonin Arc in the present study, *Stygiopontius senokuchiae* **n. sp.** was associated with populations of *Paralvinella* spp. (Annelida: Alvinellidae) and of *Neoverruca intermedia* Sha & Ren (Cirripedia: Neoverrucidae) in Myojin-sho Caldera (the type locality) (31°53'N, 139°58'E) and from populations of *Paralvinella* spp. in Myojin Knoll (32°06'N, 139°52'E). Additionally, the second and third authors collected *S. senokuchiae* **n. sp.** from bacterial mats without visible colonies of mega-benthos in Bayonnaise Knoll (31°57'N, 139°44'E) during another research cruise NT14-06 using the same research vessel and ROV. Although sampling localities in both Myojin and Bayonnaise Knolls are located about 30 km away from the type locality, it was confirmed by molecular analysis using mtCOI that all specimens are conspecific and populations in each locality might be genetically connected (H.K. Watanabe unpublished data). The hatched nauplius of a congener, *S. pectinatus*, is known to be lecithotrophic, and it is estimated that the planktonic stage released from hydrothermal fields are transported by currents and do not molt to the next stage for settlement until reaching hydrothermal fields (Ivanenko *et al.* 2007). The naupliar stages of *S. senokuchiae* **n. sp.** might use similar strategies to disperse and survive in deep sea.

On the other hand, it has been revealed by population genetics using mtCOI on some benthic crustaceans inhabiting on hydrothermal vents, such as neoverrucid barnacles and alvinocaridid shrimps, that populations are genetically connected to others on remote hydrothermal fields in western part of North Pacific Ocean (Watanabe *et al.* 2005; Yahagi *et al.* 2015). On *Stygiopontius*, it was also reported that several species were distributed across multiple seamounts however populations show high haplotype diversity and connectivity even among the different

hydrothermal fields of Pacific and Atlantic Oceans (Gollner *et al.* 2016). Further, the possibilities of larval dispersal of various animals in and between hydrothermal fields were strongly supported by the biophysical model (Mitarai *et al.* 2016). Thus, there is a possibility that *S. senokuchiae* **n. sp.** has a more ample distribution not being restricted to three seamounts, and therefore its populations may be genetically connected.

The second and third authors collected *S. senokuchiae* **n. sp.** from 742 to 1321 m depth in the calderas of the three seamounts during several research cruises (NT12-10, NT13-09, NT14-06, M. Shimanaga & H.K. Watanabe unpublished data). Since all other nominal species of *Stygiopontius* have been reported in the depth range from 1688 to 3650 m (*S. rimivagus* and *S. pectinatus*, respectively) (Humes 1987, 1997), the findings of *S. senokuchiae* **n. sp.** expand the depth range of the genus to shallower areas. This record also represents the first occurrence of the nominal species of Dirivultidae in Japanese waters.

Despite the fauna from the hydrothermal vents of Izu-Bonin Arc remains scarcely known, a species of pontocyprid Ostracoda, *Thomontocypris shimanagai* Tanaka & Yasuhara was recently described based on specimens collected during other research cruises by the third author of present study (Tanaka & Yasuhara 2016). Further, a recently described abyssochrysoid snail, *Alviniconcha adamantis* Johnson, Warén, Tunnicliffe, Van Dover, Wheat, Schultz & Vrijenhoek, was also found (Fujiwara *et al.* 2013; Johnson *et al.* 2015). Since understanding on fauna comprising hydrothermal communities of Izu-Bonin Arc is still insufficient, further discoveries of new taxa from future works are expected. A key to species of the genus *Stygiopontius* from Western Pacific is provided.

Key to species of Stygiopontius from Western Pacific

1	Leg 4 bearing seven elements (i.e., three spines plus four setae) on the third exopodal segment S. senokuchiae n. sp.
-	Leg 4 bearing eight elements (i.e., four spines plus four setae) on the third exopodal segment
2	Caudal rami less than twice long as wide
-	Caudal rami more than twice long as wide
3	Leg 4 bearing distal endopodal segment with pointed outer process S. senckenbergi Ivanenko & Ferrari, 2013
-	Leg 4 bearing distal endopodal segment without pointed processes
4	Genital double somite bearing two pairs of processes
-	Genital double somite bearing one or no pairs of processes
5	Genital double somite bearing pair of processes on posterolateral corners; basis of the leg 1 bearing an inner pointed process .
-	Genital double somite without pairs of lateral processes; basis of leg 1 without inner pointed processes

Acknowledgements

We are grateful to the captain, crews, and operation staffs of the *R/V Natsushima* and the *ROV Hyper-Dolphin* (JAMSTEC). We also thank Dr Viatcheslav N. Ivanenko (Moscow State University) for providing valuable references. Special thanks to Ms Reina Senokuchi (Kumamoto University) for helping our studies and giving us an opportunity to describe this new species. This study was partly funded by a grant from the Japan Society for the Promotion of Science Grants-in-Aid for Scientific Research (KAKENHI) program (grant number 26440246 to MS and HKW).

References

Boxshall, G.A. & Halsey, S.H. (2004) An Introduction to Copepod Diversity. The Ray Society, London, 966 pp.

Fujiwara, Y., Okutani, T. & Kimura, H. (2013) First occurrence of *Alviniconcha* from Japanese waters (Gastropoda: Provannidae). *Venus*, 71, 217–219.

Gollner, S., Ivanenko, V.N., Martínez Arbizu, P. & Bright, M. (2010) Advances in taxonomy, ecology, and biogeography of Dirivultidae (Copepoda) associated with chemosynthetic environments in the deep sea. *Plos One*, 5 (8), 1–13. https://doi.org/10.1371/journal.pone.0009801

Gollner, S., Stuckas, H., Kihara, T.C., Laurent, S., Kodami, S. & Martinez Arbizu, P. (2016) Mitochondrial DNA analyses indicate high diversity, expansive population growth and high genetic connectivity of vent copepods (Dirivultidae) across

- different oceans. *PLoS ONE*, 11 (10), 1–10. https://doi.org/10.1371/journal.pone.0163776
- Humes, A.G. (1987) Copepods from deep-sea hydrothermal vents. *Bulletin of Marine Science*, 41, 645–788. https://doi.org/10.1007/978-94-009-3103-9 63
- Humes, A.G. (1989) New species of *Stygiopontius* (Copepoda, Siphonostomatoida) from a deep-sea hydrothermal vent at the East Pacific Rise. *Zoologica Scripta*, 18, 103–113. https://doi.org/10.1111/j.1463-6409.1989.tb00125.x
- Humes, A.G. (1990) Copepods (Siphonostomatoida) from a deep-sea hydrothermal vent at the Mariane Back-Arc Basin in the Pacific, including a new genus and species. *Journal of Natural History*, 24, 289–304. https://doi.org/10.1080/00222939000770211
- Humes, A.G. (1991) Siphonostomatoid copepods from a deep-water hydrothermal zone in the Lau Basin, South Pacific. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4, Series 13, Section A1–2, 121–134.
- Humes, A.G. (1996) Deep-sea Copepoda (Siphonostomatoida) from hydrothermal sites on the Mid-Atlantic Ridge at 23°W and 37°N. *Bulletin of Marine Science*, 58, 609–653.
- Humes, A.G. (1997) Siphonostomatoid copepods from deep-sea hydrothermal sites on the Mid-Atlantic Ridge west of the Azores. *Cahiers de Biologie Marine*, 38, 63–77.
- Humes, A.G. & Dojiri, M. (1981) A new siphonostome family (Copepoda) associated with a vestimentiferan in deep water off California. *Pacific Science*, 34, 143–151.
- Humes, A.G. & Gooding, R.U. (1964) A method for studying the external anatomy of copepods. *Crustaceana*, 6, 238–240. https://doi.org/10.1163/156854064x00650
- Ivanenko, V.N. & Ferrari, F.D. (2013) New species of *Stygiopontius* (Copepoda: Siphonostomatoida: Dirivultidae) from a deepsea hydrothermal volcano in the New Ireland Fore-Arc system (Papua New Guinea). *Journal of the Marine Biological Association of the United Kingdom*, 93, 1805–1812. https://doi.org/10.1017/s0025315413000763
- Ivanenko, V.N., Martínez Arbizu, P. & Stecher, J. (2006) Copepods of the family Dirivultidae (Siphonostomatoida) from deepsea hydrothermal vent fields on the Mid-Atlantic Ridge at 14°N and 5°S. *Zootaxa*, 1277, 1–21.
- Ivanenko, V.N., Martínez Arbizu, P. & Stecher, J. (2007) Lecithotrophic nauplius of the family Dirivultidae (Copepoda; Siphonostomatoida) hatched on board over the Mid-Atlantic Ridge (5°S). *Marine Ecology*, 28, 49–53. https://doi.org/10.1111/j.1439-0485.2007.00142.x
- Johnson, S.B, Warén, A., Tunnicliffe, V., Van Dover, C., Wheat, C.G., Schultz, T.F, Vrijenhoek, R.C. (2015) Molecular taxonomy and naming of five cryptic species of *Alviniconcha* snails (Gastropoda: Abyssochrysoidea) from hydrothermal vents. *Systematics and Biodiversity*, 13, 278–295. https://doi.org/10.1080/14772000.2014.970673
- Mitarai, S., Watanabe, H., Nakajima, Y., Shchepetkinc, A.F. & McWilliams, J.C. (2016) Quantifying dispersal from hydrothermal vent fields in the western Pacific Ocean. *Proceedings of the National Academy of Sciences*, 113, 2976–2981. https://doi.org/10.1073/pnas.1518395113
- Tanaka, H. & Yasuhara, M. (2016) A New Deep-sea Hydrothermal Vent Species of Ostracoda (Crustacea) from the Western Pacific: Implications for Adaptation, Endemism, and Dispersal of Ostracodes in Chemosynthetic Systems. *Zoological Science*, 33, 555–565. https://doi.org/10.2108/zs160079
- Watanabe, H., Tsuchida, S., Fujikura, K., Yamamoto, H., Inagaki, F., Kyo, M. & Kojima, S. (2005) Population history associated with hydrothermal vent activity inferred from genetic structure of neoverrucid barnacles around Japan. *Marine Ecology Progress Series*, 288, 233–240. https://doi.org/10.3354/meps288233
- Yahagi, T., Watanabe, H., Ishibashi, J. & Kojima, S. (2015) Genetic population structure of four hydrothermal vent shrimp species (Alvinocarididae) in the Okinawa Trough, Northwest Pacific. *Marine Ecology Progress Series*, 529, 159–169. https://doi.org/10.3354/meps11267