Plankton Benthos Res 14(1): 29–38, 2019

Plankton & Benthos Research

Pseudodiaptomus yamato n. sp. (Copepoda, Calanoida) endemic to Japan, with redescriptions of the two closely related species *P. inopinus* Burckhardt and *P. japonicus* Kikuchi

Hiroshi Ueda[1,†,*] & Sakiko Orui Sakaguchi[2]

[1] *Usa Marine Biological Institute, Kochi University, 194 Inoshiri, Usa, Tosa, Kochi 781–1164, Japan*
[2] *Japan Agency for Marine-Earth Science and Technology, 2–15 Natsushima, Yokosuka, Kanagawa 237–0061, Japan*
[†] *Present address: 13–22–703 Tanaka-cho 1-chome, Higashinada-ku, Kobe 658–0081, Japan*

Received 24 August 2018; Accepted 12 November 2018 Responsible Editor: Shinji Shimode

doi: 10.3800/pbr.14.29

Abstract: The brackish-water calanoid copepod known as *Pseudodiaptomus inopinus* in the mainland of Japan consists of two genetically separate species. One is *P. japonicus*, which was once synonymized with *P. inopinus* but was recently revived. This paper describes the other species as *Pseudodiaptomus yamato* n. sp., which is confirmed to have morphological differences from *P. inopinus* s.s. based on specimens from the type locality (Lake Taihu, China) of the latter. We also redescribe *P. japonicus* and *P. inopinus* s.s. for comparative purposes. The three species are distinguishable by the combination of the following morphologies: 1) weak or prominent posterior round projections of the female last pediger; 2) relative length of posterior processes of the female genital operculum; 3) presence or absence of medial spinules on the first exopodal segment of the female leg 5; and 4) the size of spinules at the center of the ventral surface of the male second urosomite. Significant inter-population variation is observed in some spinules of *P. japonicus*. The past and present records indicate that *Pseudodiaptomus yamato* n. sp. is endemic to Japan and confined to the coasts affected by the warm Kuroshio Current from western Kyushu to the middle of Honshu, while *P. japonicus* is widespread in northern East Asia without overlapping the range of *P. yamato* n. sp. The range of *Pseudodiaptomus inopinus* s.s. most certainly does not extend to those of *P. yamato* n. sp. and *P. japonicus*.

Key words: calanoid copepod, *Pseudodiaptomus inopinus*, *Pseudodiaptomus japonicus*, *Pseudodiaptomus yamato* n. sp., taxonomy

Introduction

The calanoid copepod, previously identified as *Pseudodiaptomus inopinus* Burckhardt, 1913 in Japanese waters, is a common member of zooplankton communities in brackish waters (Sakaguchi et al. 2011). Subsequently, a species complex consisting of three allopatric sibling species has been identified (Sakaguchi & Ueda 2011) around Japan that differs from *P. inopinus* sensu stricto (s.s.). One species has already been described as *Pseudodiaptomus nansei* Sakaguchi & Ueda, 2010, and inhabits the Nansei Islands, southernmost Japan (Sakaguchi & Ueda 2010). The other two species occur around Japan's mainland, and are morphologically distinguishable by the length of the posterior processes of the female genital operculum (Sakaguchi & Ueda 2011). We previously called specimens having the shorter processes the "SP-form" and those having the longer processes the "LP-form" (Sakaguchi & Ueda 2018), or as "the Japan Sea group" and "the Pacific group" (Sakaguchi & Ueda 2011), respectively. Sakaguchi & Ueda (2018) revealed genetic divergence at the species level between these two forms, and revived the name *Pseudodiaptomus japonicus* Kikuchi, 1928 for the species of the SP-form. *Pseudodiaptomus japonicus* was erected for specimens from the Japan Sea coast of Honshu (Kikuchi 1928), but was subsequently synonymized to *P. inopinus* by Mashiko & Inoué (1952) and Ito (1965).

* Corresponding author: Hiroshi Ueda; E-mail, hueda@kochi-u.ac.jp

Sakaguchi & Ueda (2018) suggested that the LP-form is also a species distinct from *Pseudodiaptomus inopinus* s.s. Since no genetic information on *P. inopinus* s.s. is available, a morphological comparison of the LP-form based on specimens is necessary to settle the taxonomic status of the LP-form. We fortunately found *P. inopinus* s.s. specimens in the late Dr. Toshihiko Mizuno's zooplankton samples (Ueda 2016) collected from Lake Taihu, China - the type locality of this species. These specimens confirmed the distinct morphological characteristics of *P. inopinus* s.s. and allowed comparison with the LP-form. This paper describes the LP-form as the new species *Pseudodiaptomus yamato* n. sp. In addition, *P. japonicus* from Lake Suigetsu, which is one of the localities from which *P. japonicus* was first recorded (Kikuchi 1928), and *P. inopinus* s.s. from Lake Taihu are briefly redescribed to show the difference among the three species.

Materials and Methods

We collected *Pseudodiaptomus yamato* n. sp. during zooplankton surveys from 2006 to 2009 in various brackish waters of western Japan (Sakaguchi et al. 2011), ecological studies from 2003 to 2004 on estuarine copepods in the Chikugo River, northern Kyushu (Ueda et al. 2010), and our subsequent sampling in Kyushu and Shikoku. Among these localities, the Chikugo River was selected for the type locality of the new species, because specimens from there were genetically analyzed (Sakaguchi & Ueda 2018) and many adult specimens of both sexes were collected. The sample from which the type material was sorted was collected from the 2.5 m depth at the Chikugo River mouth (33.143N, 130.356E) during the daytime ebb tide on 6 August 2003. The sampling method was described by Ueda et al. (2010). The water temperature and salinity at the sampling depth measured by a temperature/salinity logger (Compact-CT, Alec Electronics) were 28.8°C and 3.1, respectively.

To investigate intraspecific variations of the new species, specimens from the following estuaries were examined (sampling date and geographic coordinates are given in parentheses): the Manose River mouth (20 August 2009; 31.4478N, 130.3087E); the Kodono River (19 September 2010; 33.4777N, 133.5150E and 20 September 2010; 33.4838N, 133.5188E); the Tama River (16 October 2010; 35.5362N, 139.7169E); and an eel-culture pond in Mie, mid-Honshu (13 October 1954, detailed location is unknown). The specimens from the Tama River were provided by Dr. Hiroshi Itoh, and those from the pond in Mie were sorted from a sample collected by the late Dr. Takashi Ito more than 60 years ago where a half volume was provided to us (HU).

Pseudodiaptomus japonicus specimens examined were collected from Lake Suigetsu (18 September 2010; 35.5786N, 135.8767E). Although the type locality of *P. japonicus* was not specified in the original description by Kikuchi (1928), Lake Suigetsu was one of the four brackish lakes where he noted the occurrence of this species; two of the other three lakes were neighboring Lakes Suga and Mikata, and the third lake was Tôgô, about 180 km west of Lake Suigetsu. The other specimens of *P. japonicus* were from the following localities: the Tsuri River mouth (18 August 2009; 33.8486N, 130.5024E), from which specimens were once identified as *P. inopinus* by Sakaguchi & Ueda (2010); the Emukae River (20 October 2010; 33.3023N, 129.6315E), the southernmost river from which *P. japonicus* has been collected in Japan; the Abashiri River (17 September 2010; 44.0041N, 144.2293E) on the Sea of Okhotsk coast of Hokkaido; and Akkeshi Bay (5 October 1982; 43.049N, 144.849E) on the Pacific coast of Hokkaido. Specimens from the last two localities were provided by Mr. Masaki Iwabuchi and Dr. Takahiko Irie, respectively.

Redescription of *Pseudodiaptomus inopinus* s.s. was made on specimens in the sample #758 from the late Dr. Mizuno's zooplankton collection (Ueda 2016). The sample was collected on 28 September 1980 from Lake Taihu, the type locality of the species (Burckhardt 1913), during the Japan-China joint survey on limnology of the Yangtze River (Mizuno 1985).

The following specimens were deposited in the National Museum of Nature and Science, Tokyo: *Pseudodiaptomus yamato* n. sp. from the Chikugo River, dissected female holotype (NSMT Cr 25864), dissected male allotype (NSMT Cr 25865), undissected 12 female and 12 male paratypes (NSMT Cr 25866 and 25867, respectively); *P. japonicus* from Lake Suigetsu, undissected 10 female and 7 male specimens (NSMT Cr 25868, 25869) and from the Akkeshi River, undissected 15 female and 10 male specimens (NSMT Cr 25870, 25871); *P. inopinus* s.s. from Lake Taihu, 1 dissected female, 2 dissected male, and 6 undissected female specimens (NSMT Cr 25872–25874). Dissected specimens were embedded in glycerol-mounted permanent slide preparations (Ueda 2018), and undissected specimens were preserved in ethanol with a glycerol drop added.

Specimens were examined on depression slides in 70% lactic acid or 50% glycerol under a differential interference contrast microscope (Nikon E600). Illustrations were prepared with the computer software package Adobe Illustrator by tracing microscope photographs taken with a digital photo-microscopic camera system (Nikon DS-5M) and/or line drawings made with a drawing tube. Body length was measured with an ocular micrometer. In specimens having an inclined or curved urosome, the urosome length was measured separately from the prosome, and then the body length was calculated by adding it to the prosome length. The length of any strongly curved female urosome was measured by combining the segment lengths. The relative length of the posterior process of the genital operculum is expressed by the ratio of the process length ('a' in Fig. 1G, measured from the base to the tip) to the distance between the tips ('b' in Fig. 1G). Illustrations of all appendages are given for the new species, but we omit some descriptions of segmentation and setation that are common to the descriptions by Sakaguchi & Ueda (2010) and Soh et al. (2012). Redescriptions of *P. japonicus* and *P. inopinus* s.s. are limited to the morphologies that differ among the present three species. Morphological terminology follows Huys & Boxshall (1991). Setal formula of the antennule is presented using the actual segment numbers, because the fusion pattern of the ancestral segments could not be definitely identified.

Systematic Accounts

Family Pseudodiaptomidae G.O. Sars, 1902
Genus *Pseudodiaptomus* Herrick, 1884

Pseudodiaptomus yamato n. sp.

(Figs. 1 and 2)

Pseudodiaptomus inopinus: Sakaguchi & Ueda (2010), fig. 7G; Sakaguchi & Ueda (2011), fig. 2B, D, F, H, J; Soh et al. (2012), fig. 3B.

Materials examined:

Female holotype, male allotype, and 9 female and 8 male paratypes from the Chikugo River; 3 females from the Manose River; 3 females and 4 males from the Kodono River; 1 male from the Tama River; 5 females and 3 males from a pond in Mie.

Description on of the type specimens:

Female—Body (Fig. 1A, B) length 1.32–1.43 mm (n=6, holotype 1.33 mm); prosome length 0.85–0.91 mm (n=6, holotype 0.85 mm). Second and third pedigers with row of fine spinules along posterolateral margin (Fig. 1C). Last pediger (Fig. 1D, E), on each side, with spiniform small dorsal attenuation, weakly protruding posterior projection, and three groups of spinules in rows, i.e., row of slightly curved, long spinules on distolateral corner (indicated by arrow with 'a' in Fig. 1E), irregular rows of medium and fine spinules on distomedial surface (indicated by arrow with 'b'), and long transverse row of fine spinules on lateral surface (indicated by arrow with 'c'). Genital double somite (Fig. 1C, F) with 2–4 fine spinules on anterolateral projection, 2 groups of a few fine dorsolateral spinules at about 1/3 and 4/5 length of somite, respectively, and fine lateral setule at mid length (Fig. 1C) on each side. Genital operculum with long posterior processes; process longer than distance between tips (Fig. 1G, 'a'>'b'). Dorsal surface of second free urosomite with transverse row of 2–5 fine spinules at about 3/5 length on each side (Fig. 1H). Caudal rami (Fig. 1I) length around 2.4 times width.

Antennule (Fig. 1J) with setal formula: 1=1+ae (aesthetasc), 2=3+ae, 3=2, 4=2+ae, 5=2+ae, 6=1 (spiniform), 7=2+ae, 8=2+ae, 9=2+ae, 10=2+ae, 11=2+ae, 12=2+ae, 13=2+ae, 14=2+ae, 15=2, 16=2, 17=2+ae, 18=2, 19=1, 20=2, 21=2, 22=6+ae. Antenna (Fig. 1K) coxa fused with basis and first endopodal segment; exopod 6-segmented, with setal formula 1, 5, 1, 1, 1, 3; second endopodal segment with 9 subterminal and 7 terminal setae. Mandible as in Fig. 1L. Maxillule praecoxa with triangular process on posterior surface (Fig. 1M, indicated by arrow). Maxilla as in Fig. 1N. Maxilliped (Fig. 1O) endopod with 4 modified setae, 2 on second segment and 1 on third segment with short branch, and 1 on fourth segment with long comb-like branch (Fig. 1P).

Leg 1 (Fig. 1Q) with 2 and 1 medially-recurved long setae on distal segments of exopod and endopod, respectively; exopod with smooth terminal spine. Legs 1–4 (Fig. 1Q–T) with fine spinules on anterior surfaces of coxa and basis, and on distal margins of first and second segments of rami. Leg 5 (Fig. 1U) coxa, fused with intercoxal sclerite, with several rows of fine spinules; basis anteriorly with 3 rows of fine spinules near lateral margin, along distal margin, and on distomedial area, respectively; first exopodal segments devoid of spinules on medial margin, with flattened round hyaline process at distomedial corner and anterior row of a few fine spinules at distolateral corner; second segment short, with lateral spine and twice-longer thick spine posteriorly; third segment weakly separated from second segment, representing medially short spine with serrate medial margin and laterally claw-like long spine.

Male—Body (Fig. 2A, B) length 1.12–1.20 mm (n=5, allotype 1.20 mm); prosome length 0.75–0.79 mm (n=5, allotype 0.78 mm). Prosome without spinular rows along distolateral margins of somites. Second to fourth urosomites fringed with conspicuous spinules throughout distal margin (Fig. 2C); second urosomite with three groups of spinules in rows, i.e., oblique lateral row (Fig. 2C, indicated by arrow), transverse ventral row at midlength of somite (Fig. 2D, indicated by arrow with 'a'), and oblique ventrolateral row posteriorly (indicated by arrow with 'b'); spinules of lateral row very fine or absent in some specimens; spinules of transverse ventral row smaller than those of ventrolateral row (Fig. 2D, E). Caudal rami (Fig. 2F) symmetrical, length 2.6–2.7 times width ('a'/'b' in Fig. 2F, n=6, allotype 2.7).

Right antennule (Fig. 2G) geniculate between 18th and 19th segments; setal formula as follows: 1=1+ae, 2=3+ae, 3=2+ae (proximal half setiform), 4=1, 5=2+ae, 6=1, 7=2+ae, 8=1 (short spine), 9=2+ae, 10=2 (1 long spine)+ae, 11=2+ae, 12=2 (1 short spine)+ae, 13=2 (1 short spine)+ae, 14=2+ae, 15=2+ae, 16=2+ae, 17=2 (1 long spine), 18=2 (1 long pine), 19=3 (1 short, 1 long spine), 20=9+2ae; 18th segment with small projection having subequal 2 tips on lateral surface and filamentous frill along anterior margin (Fig. 2H); geniculation furnished anteriorly with semi-circular hyaline plate.

Leg 5 (Fig. 2I–K) coxa, fused with intercoxal sclerite. Left leg basis, fused with endopod, forming chela bearing acute triangular process at midlength, with small seta near lateral margin, a few spinules at distolateral margin,

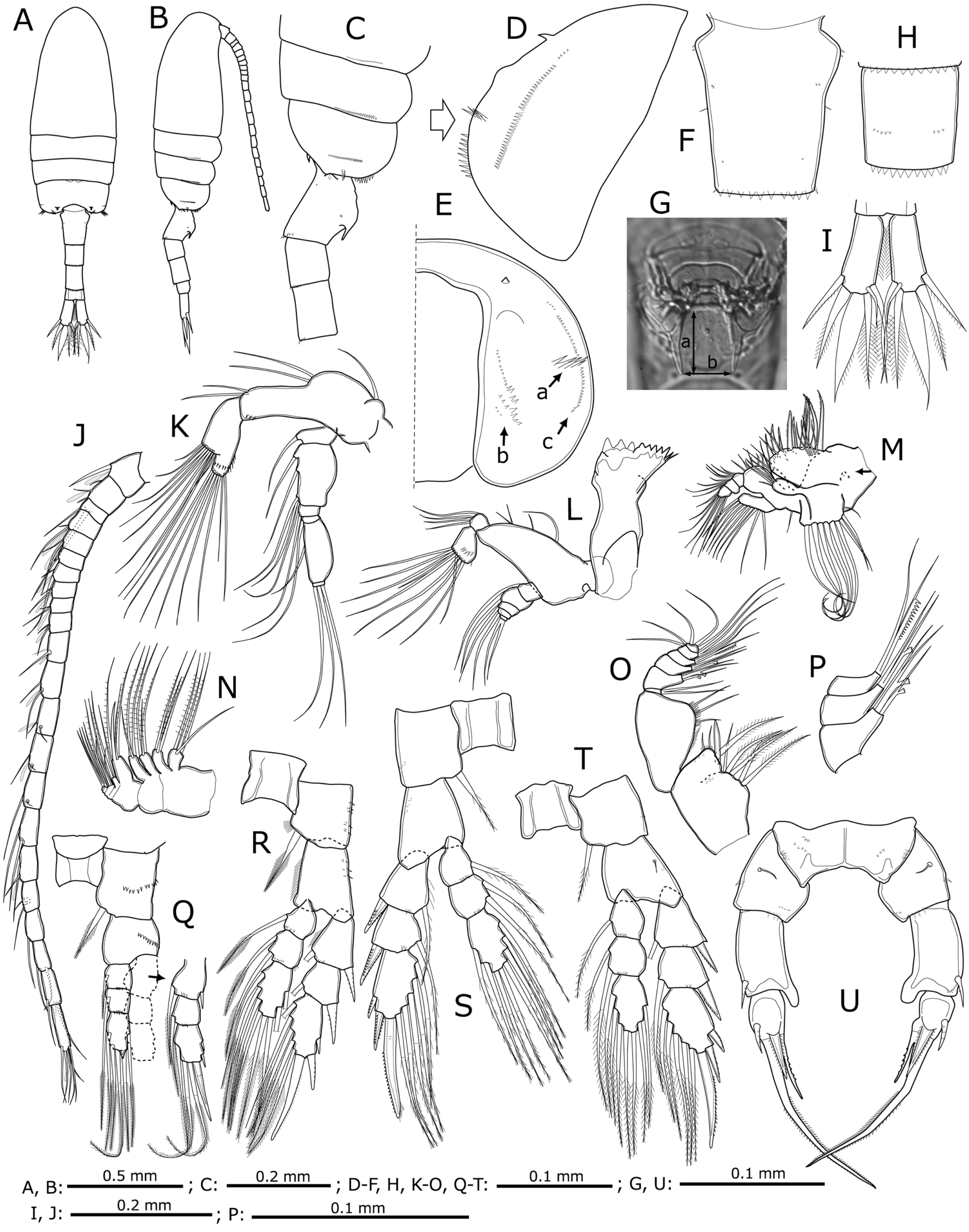

Fig. 1. *Pseudodiaptomus yamato* **n. sp.** female from the Chikugo River (A–C, F, G, I–U, holotype; D, E, H, same paratype). A, habitus, dorsal; B, habitus, lateral; C, third prosome to third urosomite; D, last pediger, lateral; E, right half of last pediger, posterior (view from indicated with a white arrow in D); F, genital double somite, dorsal; G, photograph of genital operculum, ventral; H, second urosomite with dorsal spinules; I, caudal rami, dorsal; J, left antennule; K, antenna; L, mandible; M, maxillule; N, maxilla; O, maxilliped; P, second to fourth endopodal segments of maxilliped; Q, left leg 1, anterior; R, right leg 2, posterior; S, left leg 3, posterior; T, right leg 4, posterior; U, leg 5, posterior.

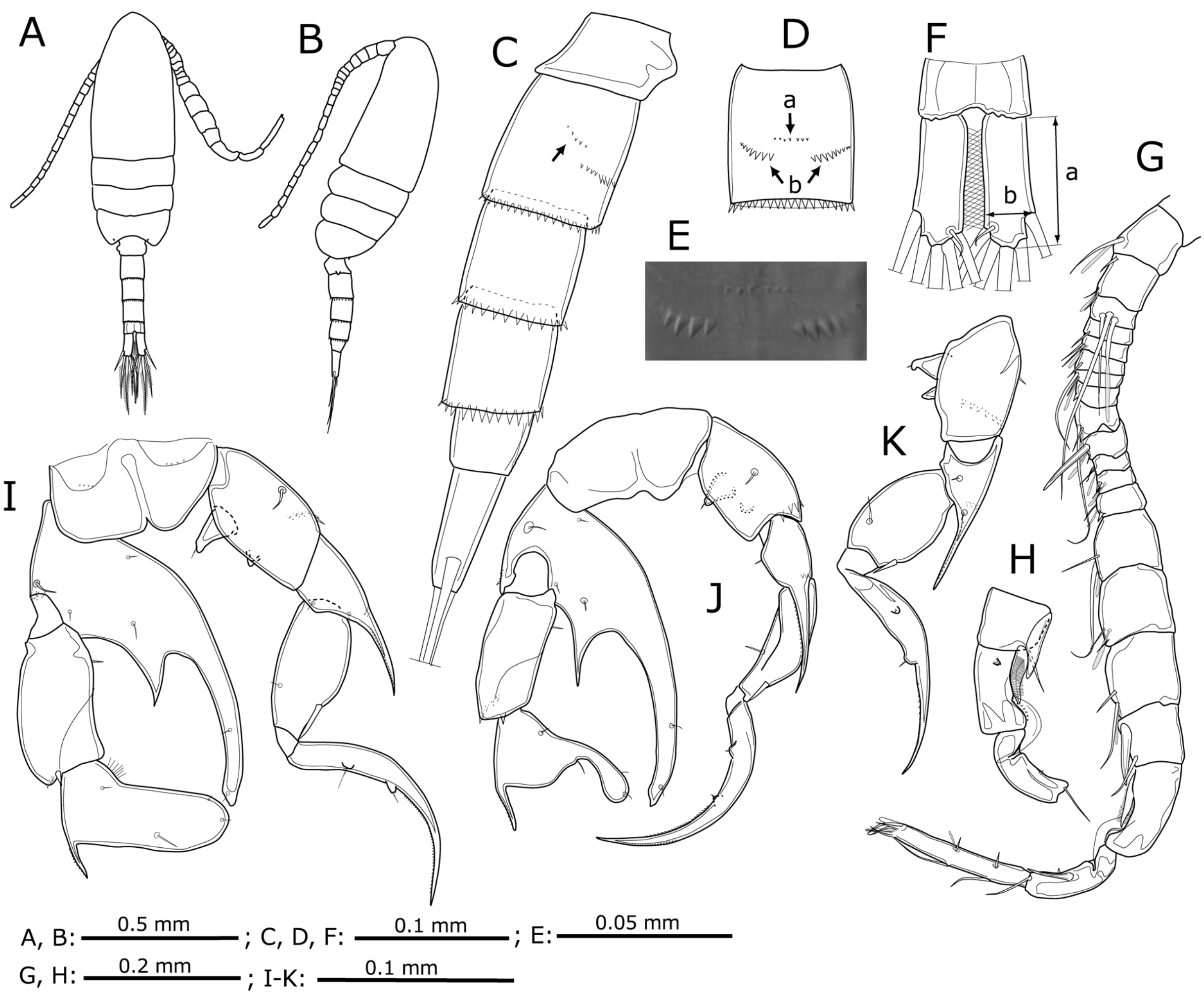

Fig. 2. *Pseudodiaptomus yamato* **n. sp.** male from the Chikugo River (A–C, F–H, allotype; D, E, I–K, 3 paratypes). A, habitus, dorsal; B, habitus, lateral; C, urosome, lateral; D, second urosomite, ventral; E, photograph of spinular rows in D; F, caudal rami, dorsal; G, right antennule, ventral; H, 19th to 21st segments of right antennule, dorsal; I, leg 5 with paddle-shaped right terminal segment, posterior; J, leg 5 with finger-shaped right terminal segment, posterior; K, right leg of J, viewed from different angle.

and 4–5 setules on posterior surface; first exopodal segment with setule proximally on medial margin, small spine on distal margin, and row of fine spinule at distolateral corner; 2nd (terminal) segment paddle-shaped (Fig. 2I) or finger-shaped (Fig. 2J), with denticulate spiniform attenuation on lateral margin, usually hairs on proximomedial part, and 4–5 posterior setules, the subterminal one very fine. Right leg uniramous; basis with small seta on posterolateral surface, 2 anteromedial processes, the proximal one of larger and bearing fine setule on tip, and spinular row on lateral surface; first exopodal segment with denticulate spiniform distal attenuation, 2 setules on posteromedial surface, and spinular row at base of attenuation; second exopodal segment somewhat flattened, with setule on posteromedial surface and spine on lateral margin; third (terminal) exopodal segment long and claw-like, denticulate on distal half, with 2 small medial processes bearing fine setule on tip, distal one of them at about midlength.

Variability:

The ranges of measurements were 1.23–1.67 mm (n=15) for the female body length, 1.10–1.30 mm (n=14) for the male body length, and 2.6–3.2 (n=12) for the length/width ratio of the male caudal ramus. Variations were observed in the number of spinules at each locus on the female last pediger, the dorsal surface of the genital double somite, and the ventral and lateral surfaces of the male second urosomite. A fine setule at each locus on the female and male leg 5 was probably missing in some specimens. However, inter-population variation of these elements was not recognized among the localities.

Etymology:

The name *yamato* is the ancient name of Japan during the Kofun period between the third and sixth centuries, when the territory of the state extended to the area from middle Honshu to northern Kyushu (Wikipedia 2018a). The geographic rage of the species is largely similar to this territory.

Remarks:

Morphological differences of *Pseudodiaptomus yamato* n. sp. from the former sibling species *P. japonicus* and *P. inopinus* s.s. are explained in the remarks of the latter two species.

Several Japanese illustrated books on plankton, e.g. Hirakawa (1997) and Mizuno (2000), describe *Pseudodiaptomus inopinus* in Japan. These descriptions are not listed as synonyms of *P. yamato* or *P. japonicus*, because the descriptions are not specific to either one of the two species, although the species in some of the illustrations can be identified by the female leg 5.

Pseudodiaptomus japonicus Kikuchi, 1928
(Fig. 3)

Pseudodiaptomus japonicus Kikuchi, 1928: 68, pl. 18, figs. 9–12, pl. 19, figs. 13–18.

Pseudodiaptomus inopinus: Smirnov (1929), 318, figs. 1–3; Mashiko & Inoué (1952), 184, fig. 8f–k; Tanaka (1966), 42, fig. 3; Kikuchi et al. (1978), 25, figs. 7–11; ?Lee et al. (2007), 140, figs. 6, 7; Sakaguchi & Ueda (2010), 62, figs. 7A–F, H, I, 8A–F; Sakaguchi & Ueda (2011), fig.

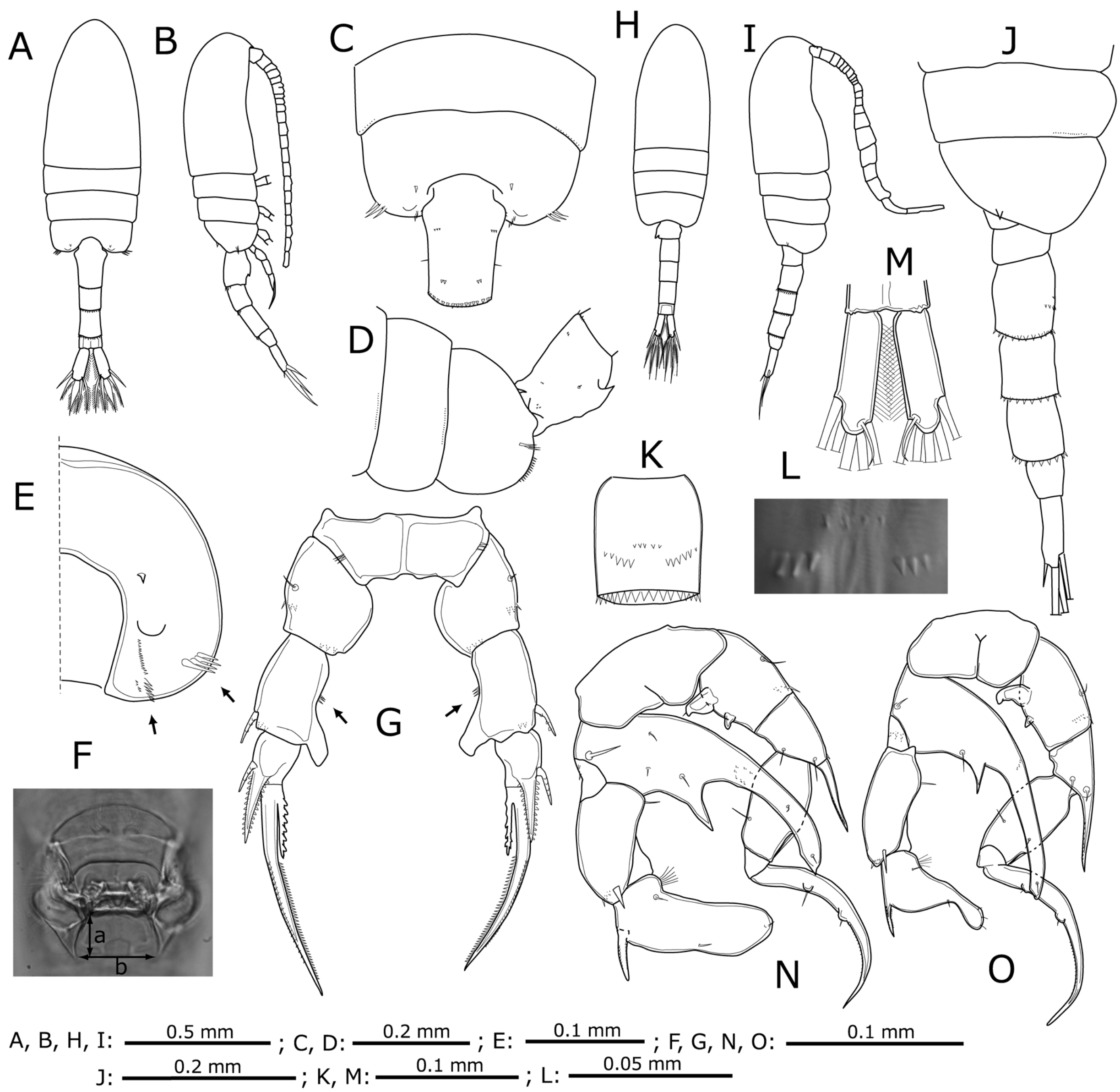

Fig. 3. *Pseudodiaptomus japonicus* female and male from Lake Suigetsu (A–G, female, H–O, male). Female: A, habitus, dorsal; B, habitus, lateral; C, D, third pediger to genital double somite, dorsal and lateral, respectively; E, last pediger, posterior; F, photograph of genital operculum; G, leg 5, posterior. Male: H, habitus, dorsal; I, habitus, lateral; J, last three pedigers and urosome, lateral; K, second urosomite, ventral; L, photograph of ventral spinular rows in K; M, caudal rami, dorsal; N, leg 5 with paddle-shaped right terminal segment, posterior; O, leg 5 with finger-shaped right terminal segment, posterior.

2A, C, E, G, I.

Pseudodiaptomus koreanus Soh et al., 2012: Soh et al. (2012), 231, figs. 2, 3A, 4–8.

Materials examined:

Five females and 9 males from Lake Suigetsu; 3 females from the Emukae River; 2 females and 2 males from the Tsuri River; 6 females and 5 males from Abashiri River; 5 females and 4 males from Akkeshi Bay.

Description of specimens from Lake Suigetsu:

Female—Body (Fig. 3A, B) length 1.19–1.26 mm (n=4); prosome length 0.75–0.84 mm (n=4). Second and third pedigers (Fig. 3C, D) with row of very fine spinules along posterolateral margin. Last pediger (Fig. 3D, E) with weakly protruded posterior projection and two groups of spinules in rows (Fig. 3E, indicated by arrows) on each side, and devoid of transverse row of fine spinules on lateral surface. Genital operculum with short posterior processes; process shorter than distance between tips (Fig. 3F, 'a'<'b'). Leg 5 with group of a few spinules (Fig. 3G, indicated by arrow) at midlength on medial margin of first exopodal segment.

Male—Body (Fig. 3H, I) length 0.96–1.19 mm (n=7); prosome length 0.66–0.75 mm (n=4). Prosome with no spinule on each somite or with very fine spinules on posterolateral margin of third pediger (Fig. 3J). Urosome (Fig. 3J–L) as in *P. yamato* n. sp. Caudal ramus (Fig. 3M) length 2.7–3.1 times width (n=4). Left leg 5 (Fig. 3N, O) with fine spinules on anterior surface of chela arm; first exopodal segment with usually concave medial margin.

Variability:

The ranges of measurements were 1.25–1.49 mm (n=13) for the female body length, 0.96–1.35 mm (n=17) for the male body length, and 2.7–3.5 (n=17) for the length/width ratio of the male caudal ramus. Inter-population variation was seen in spinular rows on the female prosome. The last pediger of the Lake Suigetsu specimens has two groups of spinules in rows on the distolateral corner and the distomedial surface, respectively, whereas females from the other four localities had three groups of spinules as described in *Pseudodiaptomus yamato* n. sp. Spinules along the posterolateral margins of the second and third pedigers were very fine in the Lake Suigetsu female specimens, whereas in the females from the other localities these were more conspicuous.

Remarks:

Pseudodiaptomus yamato n. sp. is distinguishable from *P. japonicus* by having long posterior processes of the female genital operculum and lacking medial spinules at midlength of the first exopodal segment of the female leg 5. The present study confirmed that these female morphologies are the best diagnostic characters for identification of the species, because of there being no exception among the specimens and there being easily observed.

Sakaguchi & Ueda (2011) measured the following three characters to distinguish the males: depth of medial concavity of the first exopodal segment of the left leg 5, location of the medial process on the third exopodal segment of the right leg 5, and proportional length of the caudal ramus. However, it is difficult to separate the species by these characters, because their variations overlap between the two species. In addition, the appearance of the male leg 5 depends greatly on the direction of observation (see Fig. 2J, K). The males of *P. yamato* and *P. japonicus* are not distinguishable at present.

Pseudodiaptomus inopinus specimens described from South Korea by Lee et al. (2007) probably include *P. japonicus*, because the specimens were collected from various coasts of South Korea including the east and south coasts, from which *P. koreanus* (=*P. japonicus*) was described (Soh et al. 2012). However, their specimens from the west coast are probably not *P. japonicus*, because Soh et al. (2012) indicated that specimens from the west coast are genetically different from *P. koreanus*.

***Pseudodiaptomus inopinus* Burckhardt, 1913**
(Fig. 4)

Pseudodiaptomus inopinus Burckhardt, 1913: Burckhardt (1913), 379–394, pl. 11E, figs. 2–5, 7, 8, pl. 11F, figs. 1–4, 9, 10, pl. 11G, figs. 1–4, 6–8, pl. 12H, figs. 1–4, 7, 8, 10, 11.

Schmackeria inopinus: Chen & Zhang (1965), 81–82, pl. 31, figs. 13–15; Shen & Song (1979), 69, figs. 27, 28.

Materials examined:

Two females and two males from Lake Taihu. Mizuno (1985) sampled at three stations in Lake Taihu, China, although it is unknown which station the present sample was collected from.

Description:

Female—Body (Fig. 4A, B) length 1.28 mm; prosome length 0.80 mm (n=2). Second and third pedigers with row of conspicuous spinules along posterolateral margin (Fig. 4C, D); last pediger with prominently protruding posterior projection and three groups of spinular rows on each side, i.e., row of slightly curved long spinules on distolateral corner, rows of medium or fine spinules on distomedial surface (Fig. 4E), and short row of fine spinules on lateral surface (Fig. 4D, indicated by arrow). Genital operculum with long posterior processes; process slightly longer than distance between tips (Fig. 4F, 'a'>'b'). Fifth leg (Fig. 4G, H) with group of a few spinules at midlength on medial margin of first exopodal segment.

Male—Body (Fig. 4I, J) length 1.13 mm (n=2); prosome length 0.75–0.76 mm (n=2). Second and third pedigers with row of conspicuous spinules along posterolateral margin (Fig. 4K). Second urosomite (Fig. 4L) with similar spinulation to *P. yamato* n. sp., but lateral spinular row

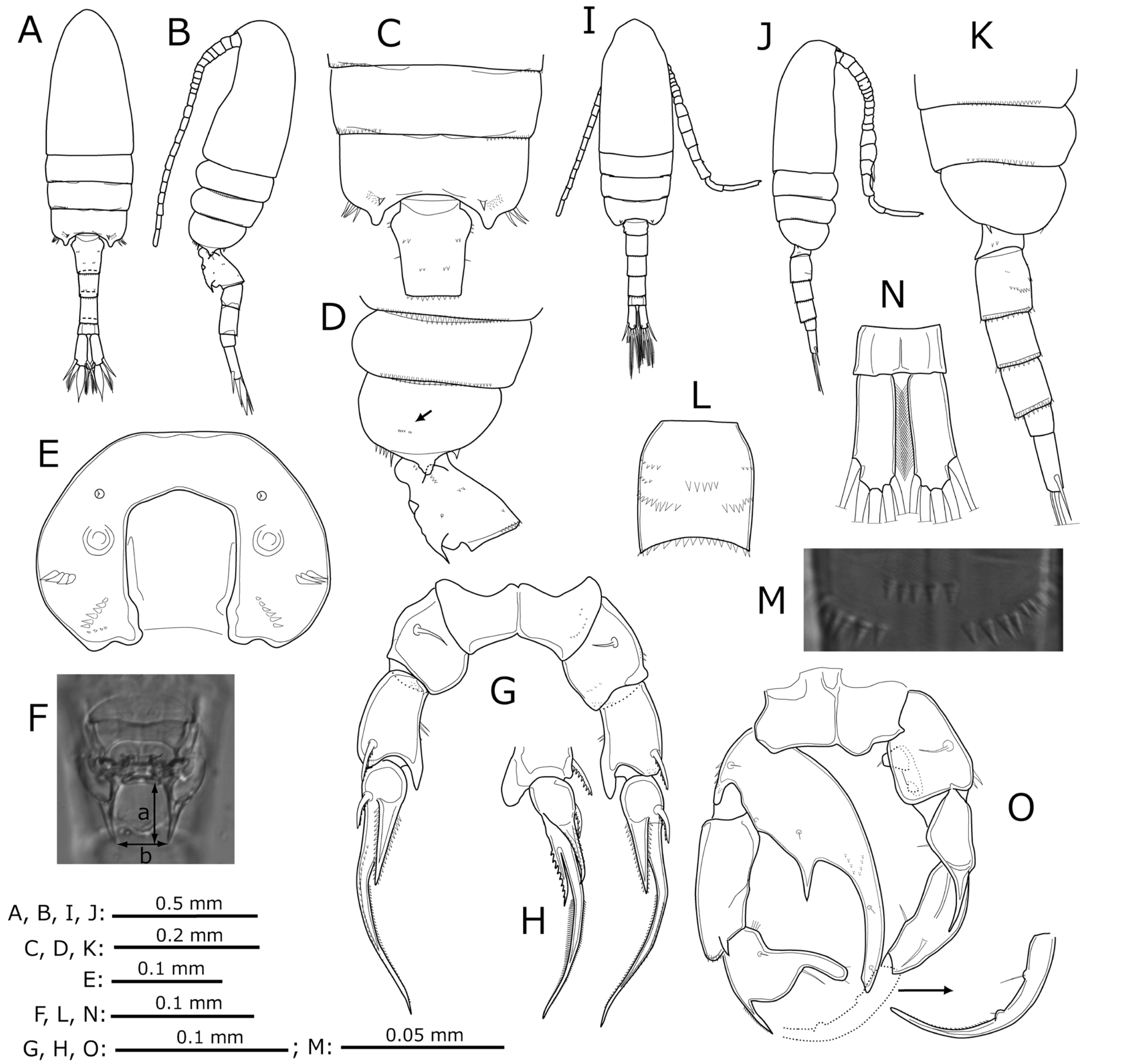

Fig. 4. *Pseudodiaptomus inopinus* female and male from Lake Taihu, China (A–H, female, I–O, male). Female: A, habitus, dorsal; B, habitus, lateral; C, D, third pediger to genital double somite, dorsal and lateral, respectively; E, last pediger, posterior; F, photograph of genital operculum; G, leg 5, posterior; H, right leg of G, viewed from a different angle. Male: I, habitus, dorsal; J, habitus, lateral; K, last three pedigers and urosome; L, second urosomite, ventral; M, photograph of ventral spinular rows in L; N, caudal rami, dorsal; O, leg 5, posterior.

more conspicuous than *P. yamato*, and spinules of transverse ventral row (Fig. 4L, M) as large as those of oblique ventrolateral row. Caudal ramus (Fig. 4N) length 2.8 times width (n=2). Left leg 5 as in Fig. 4O.

Remarks:

Pseudodiaptomus yamato n. sp. differs from *P. inopinus* s.s. by having weakly protruding posterior projections on the female last pediger and lacking medial spinules at the midlength of the first exopodal segment of the female leg 5. *Pseudodiaptomus japonicus* differs from *P. inopinus* s.s. by having the short posterior processes of the female genital operculum and the weakly protruding posterior projections on the female last pediger. The males of *P. yamato* and *P. japonicus* differ from *P. inopinus* s.s. by spinules of the transverse ventral row on the second urosomite, which are larger in *P. inopinus* s.s.

Discussion

A group of a few spinules on the medial margin of the first exopodal segment of the female leg 5 are always present in the illustrations previously assigned the name *Pseudodiaptomus inopinus* from various localities on the Japan Sea and the Tsushima (Korea) Strait coasts (Smirnov 1929, Mashiko & Inoué 1952, Tanaka 1966) and from Lake Kita-

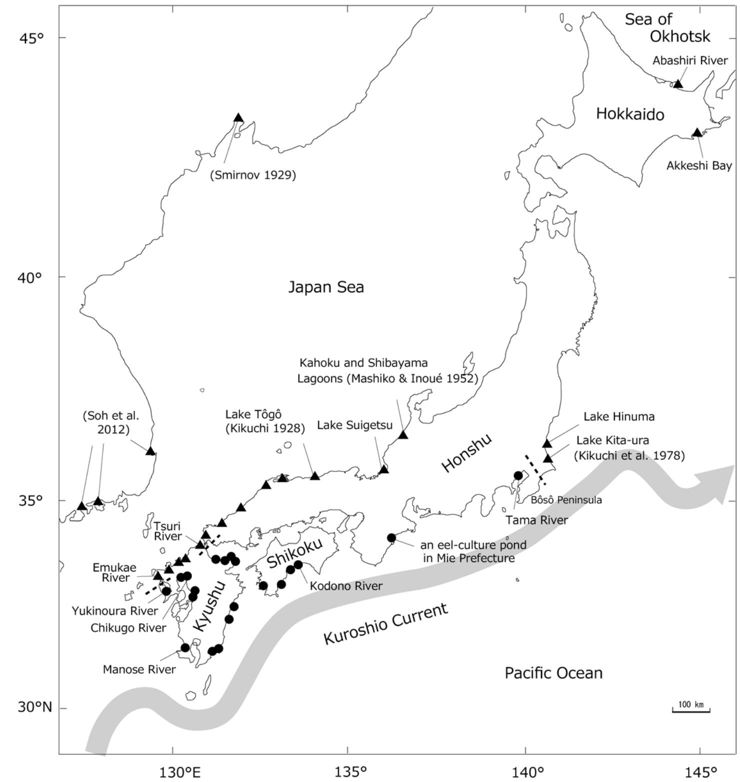

Fig. 5. Locations from which *Pseudodiaptomus yamato* n. sp. (●) and *P. japonicus* (▲) have been recorded, with the location names appearing in the text. Broken lines represent boundaries between their ranges. The references are Sakaguchi & Ueda (2010, 2011) and the present study; the other five references are presented in parentheses. Gray arrow represents the general path of the Kuroshio Current replicated from Wikipedia (2018b).

ura on the Pacific coast of Honshu (Kikuchi et al. 1978). The female last pediger in these illustrations, if present, has weakly protruding posterior projections on each side. These morphological features indicate that these illustrations are *P. japonicus*. Thus the occurrence of *P. japonicus* on the Sea of Okhotsk and the Pacific coasts of Hokkaido as well as the whole coast of the Japan Sea (Fig. 5) indicates that the species is widespread in northern East Asia. In contrast, *Pseudodiaptomus yamato* n. sp. is apparently endemic to Japan and is confined to the warm Kuroshio Current coasts of the middle and western mainland of Japan. The geographical ranges of the two species do not overlap each other with narrow boundaries at the northeast coast of Kyushu, a small strait between Kyushu and Honshu, and the Bôsô Peninsula, middle Honshu.

Although *Pseudodiaptomus inopinus* has been recorded from various localities on the Chinese continental coast (Shen & Song 1979), known localities where *P. inopinus* s.s. was described with original illustrations are only the type locality Lake Taihu (Burckhardt 1913) and a sea near Fengxian District (Chen & Zhang 1965), which is near the type locality. Therefore, the range of *P. inopinus* s.s. is still uncertain. However, it is most certain that the range of *P. inopinus* s.s. does not extend to the Japan Sea and around the mainland of Japan, because all illustrations of the *P. inopinus* species complex so far described from these regions are assignable to either *P. japonicus* or *P. yamato* n. sp.

The major factor separating the geographic ranges of *Pseudodiaptomus yamato* n. sp. and *P. japonicus* is probably the difference in temperature preference between the two species. *Pseudodiaptomus yamato* prefers high temperatures, and shows clear seasonal changes in the Chikugo River estuary with a maximum in summer and a minimum in winter (Suzuki et al. 2012). On the contrary, *P. japonicus* probably prefers low temperatures. For example, high densities in a brackish-water system on the Japan Sea coast of western Honshu were recorded mostly in winter, when the water temperature was <10°C (Uye et al. 2000).

Pseudodiaptomus koreanus, described from eastern and southern South Korea, is a synonym of *P. japonicus* (Sakaguchi & Ueda 2018). According to the illustrations of *P. koreanus* (Soh et al. 2012), however, spinular rows are more remarkable than those of *P. japonicus* in Japan. For example, Korean males have conspicuous spinular rows along the posterolateral margins of the pedigers, whereas in Japanese males the posterolateral margins of the pedigers lack spinular rows. Such inter-population variation was also observed in the spinular rows on the last pediger of females between Lake Suigetsu and the other localities in Japan. Compared with variations in these spinules, the medial spinules on the first exopodal segment of the female leg 5, which are much less numerous and not so conspicuous, do not exhibit inter-population variation. This suggests that genetic stability of spinules is not related to the spinule size and number.

Acknowledgements

We are indebted to Mr. Masaki Iwabuchi of Econixe Co. Ltd. for providing us the specimens from the Abashiri River, Dr. Takahiko Irie of the Hokkaido National Fisheries Research Institute (at that time) for providing zooplankton samples from Akkeshi Bay, and Dr. Makoto Nagoshi of Mie University (at that time) for providing the late Dr. Takashi Ito's sample, Dr. Susumu Ohtsuka of Hiroshima University for his valuable comments on terminology, and two anonymous reviewers for helpful suggestions.

References

Burckhardt G (1913) Zooplankton aus ost- und süd-asiatischen Binnengewässern. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 34: 341–471. (in German)

Chen Q, Zhang S (1965) The planktonic copepods of the Yellow Sea and the East China Sea I. Calanoida. Studia Marina Sinica 7: 20–131, pls.1–53. (in Chinese)

Hirakawa K (1997) Family Pseudodiaptomidae. In: An Illustrated Guide to Marine Plankton in Japan (eds Chihara M, Mizuno M). Tokai University Press, Tokyo, pp. 893–897. (in Japanese)

Huys R, Boxshall GA (1991) Copepod Evolution. The Ray Society, London, 468 pp.

Ito T (1965) *Pseudodiaptomus inopinus*. In: New Illustrated Encyclopedia of the Fauna of Japan (Middle Volume). Hokuryu-Kan Publishing Co. Ltd., Tokyo, p. 469. (in Japanese)

Kikuchi K (1928) Freshwater Calanoida of middle and south-western Japan. Mem Coll Sci, Kyoto imp Univ, Ser B 4: 65–79, pls 18–22.

Kikuchi Y, Yoshida R, Yamane S (1978) A faunistic survey of the calanoid and cyclopoid copepods (Class Crustacea) from Lake Kita-ura, Ibaraki Pref. Bull Fac Edu Ibaraki Univ (Natur Sci) 27: 21–46. (in Japanese with English abstract)

Lee JM, Yoon HJ, Chang CY (2007) A faunistic study on the brackish-water calanoid copepods from South Korea. Korean J Syst Zool 23: 135–154.

Mashiko K, Inoué A (1952) Limnological studies of the brackish-water lakes in the Hokuriku District, Japan. Special Publication of the Japan Sea Regional Fisheries Research Laboratory, 3rd Anniversary of Its Founding, pp. 175–191.

Mizuno T (1985) Freshwater plankton fauna and flora in the middle part of the Yangtze River. Bull Osaka Aoyama Junior College 12: 235–248. (in Japanese)

Mizuno T (2000) Order Calanoida. In: An Illustrated Guide to Freshwater Zooplankton in Japan (eds Mizuno T, Takahashi E). Tokai University Press, Tokyo, pp. 2–16. (in Japanese)

Sakaguchi SO, Ueda H (2010) A new species of *Pseudodiaptomus* (Copepoda: Calanoida) from Japan, with notes on the closely related *P. inopinus* Burckhardt, 1913 from Kyushu Island. Zootaxa 2623: 52–68.

Sakaguchi SO, Ueda H (2011) Morphological divergence of *Pseudodiaptomus inopinus* Burckhardt, 1913 (Copepoda: Calanoida) between the Japan Sea and Pacific coasts of western Japan. Plankton Benthos Res 6: 124–128.

Sakaguchi SO, Ueda H (2018) Genetic analysis on *Pseudodiaptomus inopinus* (Copepoda, Calanoida) species complex in Japan: revival of the species name of *P. japonicus* Kikuchi, 1928. Plankton Benthos Res 13: 173–179.

Sakaguchi SO, Ueda H, Ohtsuka S, Soh HY, Yoon YH (2011) Zoogeography of planktonic brackish-water calanoid copepods in western Japan with comparison with neighboring Korean fauna. Plankton Benthos Res 6: 18–25.

Shen CJ, Song DX (1979) Calanoida, Sars, 1903. In: Fauna Sinica, Crustacea, Freshwater Copepoda (ed Research Group of Carcinology, Institute of Zoology, Academia Sinica). Science Press, Beijing, pp. 53–163. (in Chinese)

Smirnov SS (1929) Beiträge zur Copepodenfauna Ostasiens. Zool Anz 81: 317–329.

Soh HY, Kwon SW, Lee W, Yoon YH (2012) A new *Pseudodiaptomus* (Copepoda, Calanoida) from Korea supported by molecular data. Zootaxa 3368: 229–244.

Suzuki KW, Ueda H, Nakayma K, Tanaka M (2012) Different patterns of stage-specific horizontal distribution between two sympatric oligohaline copepods along a macrotidal estuary (Chikugo River, Japan): implications for life-history strategies. J. Plankton Res 34: 1042–1057.

Tanaka O (1966) Neritic Copepoda Calanoida from the northwest coast of Kyushu. Proc Symp Crustacea (Part 1), 38–50.

Ueda H (2016) The late Dr. Toshihiko Mizuno's freshwater zooplankton samples. Bull Plankton Soc Jpn 63: 21–22. (in Japanese with English abstract)

Ueda H (2018) Newly devised glycerol-mounted permanent slide preparation for dissected specimens of micro-crustaceans. Plankton Benthos Res 13: 28–31.

Ueda H, Kuwatani M, Suzuki KW (2010) Tidal vertical migration of two estuarine copepods: naupliar migration and position-dependent migration. J Plankton Res 32: 1557–1572.

Uye S, Shimazu T, Yamamuro M, Ishitobi Y, Kamiya H (2000) Geographical and seasonal variations in mesozooplankton abundance and biomass in relation to environmental parameters in Lake Shinji–Ohashi River–Lake Nakaumi brackish-water system. J Mar Syst 26: 193–207.

Wikipedia (2018a) History of Japan. Available at https://en.wikipedia.org/wiki/History_of_Japan. (accessed on 1 July 2018)

Wikipedia (2018b) Kuroshio Current. Available at https://en.wikipedia.org/wiki/Kuroshio_Current. (accessed on 1 July 2018)