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Rediscovery of the Red-and-White Commensal Shrimp *Athanopsis dentipes* (Alpheidae), Revealing an Expanded Host Range Among Spoon Worms (Annelida: Thalassematidae)

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The commensal shrimp genus *Athanopsis* Coutière, 1897 (Alpheidae) includes nine species worldwide. Almost all congeners have been confirmed to be associated with spoon worms (Annelida: Thalassematidae). *Athanopsis dentipes* Miya, 1980 was originally described about 45 years ago based only on the male specimens collected along with the thalassematid spoon worm *Anelassorhynchus* cf. *mucosus* (Ikeda, 1904) in Kyushu Island, western Japan. However, it has never been collected since its original description. In this study, we rediscovered this species in the intertidal zone of the southern Kii Peninsula, Wakayama Prefecture, central Japan, and redescribed it based on both male and female specimens. Morphologically, this species is distinguished from its closest relative, *Athanopsis australis* Banner and Banner, 1982, by its ventrally straight rostrum, a large tooth at the cutting edge on the dactylus of major chela, and a small subacute tooth at the ventrolateral distal angle on the merus of third pereopod. All of the specimens were associated with thalassematid hosts, including two genera and four species of Thalassematini—i.e., *Listriolobus* cf. *sorbillans* (Lampert, 1883) and three species of *Anelassorhynchus* Annandale, 1922—substantially expanding the known host range of this shrimp species. The shrimps were observed to scuttle over the body surface of the host in the aquaria. One male–female pair was collected from the same host in February, and two ovigerous females were collected in February and April.

Key words: COI, commensalism, Echiura, host shift, symbiosis, haplotype network

INTRODUCTION

Alpheidae, a caridean family whose members are commonly known as snapping shrimps, is one of the largest decapod families, consisting of 52 genera (DecaNet eds., 2025). Most species of alpheid shrimps are found in shallow waters, whereas others occur in diverse environments, such as the deep sea and freshwater (e.g., Banner and Banner, 1978, 1983; Yeo and Ng, 1996). Shrimps in certain alpheid genera are capable of producing sounds through the rapid closure of their first pereopod (Versluis et al., 2000; Kaji et al., 2018). Interestingly, many species are known to be asso-

ciated with other benthic animals, including gobies, sponges, sea anemones, corals, and spoon worms (Annelida: Thalassematidae) (e.g., Bruce, 1976; Banner and Banner, 1982; Anker et al., 2005; Goto and Kato, 2012; Hurt et al., 2013; Henmi et al., 2017).

The genus *Athanopsis* Coutière, 1897 consists of nine species: *Athanopsis australis* Banner & Banner, 1982; *Athanopsis brevirostris* Banner & Banner, 1981; *Athanopsis dawa* Anker, 2023; *Athanopsis dentipes* Miya, 1980; *Athanopsis gotoi* Anker, 2012; *Athanopsis platyrhynchus* Coutière, 1897; *Athanopsis rubricincta* Berggren, 1991; *Athanopsis saurus* Anker, 2011; and *Athanopsis tarahomii* Marin, Sheibani & Sari, 2014. Within this genus, seven species are definitively known to be associated with thalassematids (Table 1). *Athanopsis brevirostris* was initially

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Table 1. Summary of known associations between species of the genus *Athanopsis* and their thalassematid hosts.

Species	Host echiuran(s)/associated animal(s)	Locality	Reference
<i>Athanopsis australis</i>	<i>Anelassorhynchus porcellus</i> , <i>Tastrypaea poorei</i> (as <i>Biffarius poorei</i>) (ghost shrimp)	Victoria, Eastern Australia	Banner and Banner (1981); Anker and Ahyong (2007); Edmunds et al. (2012)
<i>Athanopsis brevirostris</i>	<i>Ochetostoma erythrogrammon</i> , <i>Ochetostoma</i> sp. (not <i>Listriolobus</i> sp.)	Madagascar, Southern Red Sea, Ryukyu Islands	Banner and Banner (1981); Miya (1984); Anker (2012, 2023); Goto (2017)
<i>Athanopsis dawa</i>	presumably from echiuran burrows	Masirah Island, Oman	Anker (2023)
<i>Athanopsis dentipes</i>	<i>Anelassorhynchus mucosus</i>	Kyusyu Island, Japan	Miya (1980)
<i>Athanopsis gotoi</i>	<i>Anelassorhynchus</i> sp. 2 (as <i>Ochetostoma erythrogrammon</i>), <i>Ochetostomatinae</i> gen. sp.	Ryukyu Islands, Japan, Beo Island, Indonesia	Anker (2012); Goto (2017)
<i>Athanopsis platyrhynchus</i>	none observed (possibly free-living)	Djibouti	Coutière (1897, 1899)
<i>Athanopsis rubricinctuta</i>	<i>Ochetostomatinae</i> gen. sp., <i>Ochetostoma</i> sp.	Mozambique, Masirah Island, Oman	Berggren (1991); Anker (2023)
<i>Athanopsis saurus</i>	<i>Anelassorhynchus</i> sp. (as <i>Ochetostoma</i> sp.)	Great Barrier Reef, New Caledonia	Anker (2011, 2023)
<i>Athanopsis tarahomii</i>	Echiura gen. sp., <i>Ochetostoma</i> sp.	Iran, Saudi Arabia	Marin et al. (2014); Anker (2023)

described from shallow-water coral rubble in the southern Red Sea (Banner and Banner, 1981), although its host was unknown. Subsequently, this species was collected with its host thalassematid *Ochetostoma erythrogrammon* Rüppell and Leuckart, 1828 (as *Ochetostoma* sp.) in the Ryukyu Islands (Anker, 2012; Goto, 2017). Two additional specimens of *At. brevirostris* were recorded from a single burrow in Madagascar, although their hosts were not collected together with them (Anker, 2012). More recently, this species was collected together with an unidentified species of *Ochetostoma* in the Red Sea (Anker, 2023). Berggren (1991) described *At. rubricinctuta* from Mozambique in association with a thalassematid echiuran belonging to the subfamily *Ochetostomatinae*. Anker (2023) reported on the association between *At. rubricinctuta* and an unidentified species of *Ochetostoma* in Masirah Island, Oman (Anker, 2023). According to Anker (2011), *At. saurus* was originally reported from sand-flat coral rubble in the Great Barrier Reef, with no evidence of association with other organisms observed at the time. Later, Anker (2023) collected *At. saurus* in New Caledonia in association with a thalassematid, *Ochetostoma* sp. In the original description, *At. australis* was found within sandy sediment at a depth of approximately 8 m in eastern Australia (Banner and Banner, 1981; Anker and Ahyong, 2007). Edmunds et al. (2012) collected *At. australis* using an air-lift suction sampler in Victoria, Australia. In this survey, shrimps were collected with a thalassematid, *Anelassorhynchus porcellus* Fisher, 1948, and a burrowing ghost shrimp, *Tastrypaea poorei* (as *Biffarius poorei*) (Callianassidae). *Athanopsis gotoi* was found in association with *Anelassorhynchus* sp. 2 sensu Goto et al. (2020) (originally misidentified as *O. erythrogrammon*) from the Ryukyu Islands, Japan and an unidentified species of *Ochetostoma* from Beo Island, Indonesia (Anker, 2012; Goto, 2017). Marin

et al. (2014) reported *At. tarahomii* from Iran. Afterward, Anker (2023) collected *At. tarahomii* associated with *Ochetostoma* sp. in Saudi Arabia. As for the remaining two species, *At. dawa* and *At. platyrhynchus*, their biology remains unknown in detail; however, at least *At. dawa* was collected from animal burrows presumed by Anker (2023) to be those of thalassematids in a sandflat in Masirah Island, Oman. *Athanopsis platyrhynchus* was originally described based on material collected from beneath stones in sand in Djibouti (Coutière, 1897, 1899). Subsequently, Miya (1984) recorded *At. platyrhynchus* from Pohnpei, but Anker (2012) corrected this identification as *At. brevirostris*. There have been no records of host species of *At. platyrhynchus*.

Athanopsis dentipes (Japanese name: murasaki-ebi-modoki) was originally described based on two male specimens from western Kyushu, Japan (Miya, 1980). The holotype inhabited a burrow of the thalassematid *Anelassorhynchus* cf. *mucosus* (Ikeda, 1904) (as *Thalassema ?mucosa*), while the paratype was free living, found among night samples collected from Amakusa, Kumamoto Prefecture (Miya, 1980). Later, Miya (1995) noted that the actual host of the holotype of *At. dentipes* was *Urechis unicinctus* (Drasche, 1880), though this assertion remains subject to debate (Anker et al., 2005). Given that the species identity of *An. mucosus* itself is also ambiguous (Goto, 2017), the host of *At. dentipes* remains uncertain.

Except for the original description, *At. dentipes* has been recorded only from Komesu, Itoman, Okinawa Island, Japan (Yoshigou and Nakamura, 2005), although no information on the morphology of the voucher specimen is available.

In this study, we rediscovered *At. dentipes* from the Pacific coast of Honshu Island, Japan, found in association with various thalassematid hosts. We redescribe the species, documenting the female morphological characters for

the first time and providing genetic data derived from the mitochondrial cytochrome *c* oxidase subunit I (COI). Furthermore, we have identified its host thalassematids based on morphological and genetic data. The specimen identified with *At. dentipes* by Yoshigou and Nakamura (2005) has been reexamined and its identity is clarified.

MATERIALS AND METHODS

Field sampling and morphological examination

Specimens of *At. dentipes* and their thalassematid hosts were collected from Kushimoto and Shirahama, Wakayama Prefecture, southern Kii Peninsula, central Japan (Fig. 1A, B). In total, two specimens (SMBL-V0873 and SMBL-V0878) were collected from Shirahama, and five specimens (SMP-2198, SMBL-V0874, SMBL-V0875, SMBL-V0876, and SMBL-V0877) were collected from Kushimoto (Table 2). Each specimen was collected from beneath different stones embedded in sand within the intertidal zone of a rocky shore. Shrimps were fixed and preserved in 99% ethanol after being relaxed in $MgCl_2$ solution for photography. Host thalassematid specimens were fixed in 10% formalin solution after being relaxed in $MgCl_2$ solution. A small piece of tissue was excised from each specimen prior to formalin fixation and preserved in 99% ethanol for molecular analyses. Specimens examined in this study are deposited in the following institutions: the Museum of Seto Marine Biological Laboratory (SMBL) and the Sabiura Marine Park Research Station (SMP), Kushimoto, Japan (Table 2). The speci-

men identified as *At. dentipes* by Yoshigou and Nakamura (2005) is deposited in the Hiwa Museum of Natural History. The putative names of the thalassematid genus *Anelassorhynchus* Annandale, 1922 follow Goto et al. (2020).

Images of the shrimps and their host thalassematids were taken with digital single-lens reflex cameras (Tough TG-5, Olympus, Japan; EOS Kiss x6i, Canon, Japan) and a binocular stereo microscope (SMZ18, Nikon, Japan). The total length (tl.) of all shrimps was measured using ImageJ from the tip of the rostrum along the dorsal margin to the posterior margin of the telson (measurements were done on the curved body), carapace length (cl.) was measured from the tip of the rostrum to the posterior margin of the carapace. Shrimp specimens were dissected under a binocular stereomicroscope (SMZ18, Nikon, Japan) and some shrimps were sketched. Line drawings were made using a drawing tube (Y-IDT, Nikon, Japan) attached to a light microscope (Eclipse E600, Nikon, Japan). Two male shrimps (SMP-2198, SMBL-V0878) and one female shrimp (SMBL-V0874) were used for morphological illustration.

Behavioral observation

Athanopsis dentipes (SMBL-V0874–V0876) and its host thalassematids were transported alive to Seto Marine Biological Laboratory, Kyoto University, and kept in a plastic tray for observation. Four shrimps and two thalassematids were placed away from each other in a plastic tray as simple separation trials. A total of four shrimps and three thalassematids were examined, as follows: three shrimps (SMBL-V0875–V0877) and their two thalassematid hosts collected in Kushimoto, and one shrimp (SMBL-V0878) and its thalassematid host collected in Shirahama. To compare host utilizing patterns, a similar trial was conducted on the thalassematid-symbiotic snapping shrimp *Alpheus barbatus* Coutière, 1897, using two shrimps collected from *Anelassorhynchus* sp. 10 sensu Goto et al. (2020) in Shirahama and one shrimp collected from *Anelassorhynchus* sp. 12 sensu Goto et al. (2020) in Kushimoto.

DNA extraction, PCR, and sequencing

The genomic DNA was extracted from the tissue of pleopods (mainly fourth pleopod) of *At. dentipes* and the tissue of the proboscis of their host thalassematids using DNeasy Blood and Tissue Kits (Qiagen, Germantown, MD, USA) following the manufacturer's protocol. A total of six shrimps and five thalassematids were examined (Table 2). The polymerase chain reaction was performed using the primers LCO1490 and HCO2198 (Folmer et al., 1994), following the protocol in Goto et al. (2024). The PCR products were purified with ExoSAP-IT Express PCR Cleanup Reagent (Thermo Fisher Scientific K.K., Tokyo, Japan) and then sent to Eurofins Genomics (Tokyo, Japan) with the PCR primers for sequencing.

DNA analysis

The obtained sequences were aligned with the software SeaView v5.0.4 (Galtier et al., 1996; Gouy et al., 2010). The maximum likelihood (ML) tree of host thalassematids was reconstructed based on the newly generated COI gene sequences (Table 2), together with sequences of *L. sorbillans* (AB968033 from Tanaka et al., 2014; Kabira Bay, Ishigaki Island, Japan) and *Arhynchite hayaoi* (AB771495 from Goto et al., 2013; Kure, Hiroshima, Japan), included for comparison and as an outgroup, respectively, using RAXML HPC through raxml GUI 2.0 (Edler et al., 2021). The GTR + GAMMA substitution model was applied, and 1000 bootstrap replications were performed to evaluate the reliability of the nodes (Felsenstein, 1985). The haplotype network of *At. dentipes* was constructed using a median joining network analysis based on COI alignments in PopART (Leigh and Bryant, 2015).

RESULTS

Field observation

All shrimps were collected from the body surface or bur-

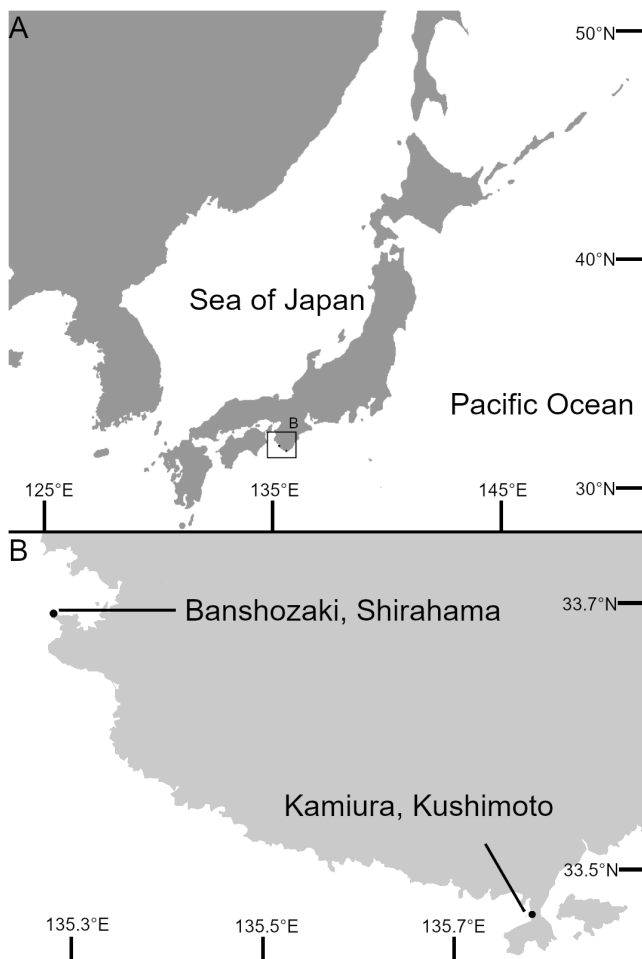


Fig. 1. Geographic location of the sampling sites. (A) Japan, (B) Southern Kii Peninsula.

Table 2. Collection and host data for specimens of *Athanopsis dentipes*. Information includes specimen number, GenBank accession number of COI sequence data, carapace length, body length, sex, sampling details, host species, host GenBank accession number of COI sequence data, and 'No. of pairs per host' column indicates specimens collected as a male–female pair from the same individual host.

Number	GenBank accession number	Carapace length (mm)	Body length (mm)	Sex	Sampling date	Sampling locality	Latitude	Longitude	Host	Host GenBank accession number
SMP-2198	–	6.1	16.0	male	June 2011	Kamiura, Kushimoto, Wakayama Prefecture, Japan	33°27'46"N	135°46'34"E	<i>Anelassorhynchus</i> sp.	–
SMBL-V0873	LC910706	4.9	13.6	female	27 Apr 2025	Banshozaki, Shirahama, Wakayama Prefecture, Japan	31°14'48"N	130°26'05"E	<i>Anelassorhynchus</i> sp. 12 sensu Goto et al. (2020)	LC910712
SMBL-V0874	LC910707	6.0	15.5	ovigerous female	31 Mar 2021	Kamiura, Kushimoto, Wakayama Prefecture, Japan	33°27'46"N	135°46'34"E	<i>Listriolobus</i> cf. <i>sorbillans</i>	LC910713
SMBL-V0875	LC910708	5.2	14.4	ovigerous female	1 Feb 2023	Kamiura, Kushimoto, Wakayama Prefecture, Japan	33°27'46"N	135°46'34"E	<i>Anelassorhynchus</i> sp. 9 sensu Goto et al. (2020)	LC910714
SMBL-V0876*	LC910709	5.4	14.7	male	3 Feb 2023	Kamiura, Kushimoto, Wakayama Prefecture, Japan	33°27'46"N	135°46'34"E	<i>Anelassorhynchus</i> sp. 10 sensu Goto et al. (2020)	LC910715
SMBL-V0877*	LC910710	5.2	14.2	ovigerous female	3 Feb 2023	Kamiura, Kushimoto, Wakayama Prefecture, Japan	33°27'46"N	135°46'34"E	<i>Anelassorhynchus</i> sp. 10 sensu Goto et al. (2020)	LC910715
SMBL-V0878	LC910711	4.6	12.0	male	28 May 2025	Banshozaki, Shirahama, Wakayama Prefecture, Japan	31°14'48"N	130°26'05"E	<i>Anelassorhynchus</i> sp. 12 sensu Goto et al. (2020)	LC910716

*These individuals were observed as a pair.

row of the thalassematid hosts living beneath different stones embedded in the bottom sediments. In detail, shrimps collected in Kushimoto were associated with three species of thalassematids, *Anelassorhynchus* sp. 9 sensu Goto et al. (2020), *An.* sp. 12 sensu Goto et al. (2020) and *L.* cf. *sorbillans*, in Kamiura Beach, Kushimoto. Also, shrimps collected in Shirahama were associated with one thalassematid species, *Anelassorhynchus* sp. 10 sensu Goto et al. (2020) (Figs. 2B, D–F, 3A, B). Two male (SMP-2198, SMBL-V0878) and three female (SMBL-V0873, V0874, V0875) shrimps were collected solitary, each occupying a separate burrow. In contrast, a single male (SMBL-V0876)–female (SMBL-V0877), pair occupying the same burrow was collected in Kushimoto during the survey on 3 February 2023 (Table 2).

Haplotype network and genetic divergence of *Athanopsis dentipes*

Figure 4 illustrates the haplotype network of *At. dentipes* based on their COI gene sequences. The haplotype network contained four haplotypes. No clear genetic structure was detected corresponding to each host species or genus.

There was only a maximum difference of 0.6% in the K2P genetic distances among the individuals.

Redescription of *Athanopsis dentipes*

***Athanopsis dentipes* Miya, 1980**
(Figs. 2, 3, 6–10; Table 2)

Athanopsis dentipes: Miya, 1980, 118–125, figs. 1–3; Miya, 1995, 322, fig. 21–257; Hayashi, 1996: 496, fig. 314.
Not *Athanopsis dentipes*: Yoshigou and Nakamura, 2005, 61. = *Arete dorsalis* Stimpson, 1860.

Material examined

SMP-2198, male, tl. 16.0 mm, cl. 6.1 mm, Kushimoto, Wakayama Prefecture, Japan, 33°27'46" N, 135°46'34" E, coll. M. Tanaka, June 2011, host: *Anelassorhynchus* sp. (host specimen not collected). SMBL-V0873, female, tl. 13.6 mm, cl. 4.9 mm, Shirahama, Wakayama, Japan, 33°41'40.9" N, 135°20'10.0" E, coll. T. Hanaoka, 27 April 2025, GenBank accession number: LC910706, host: *An.* sp. 12 sensu Goto

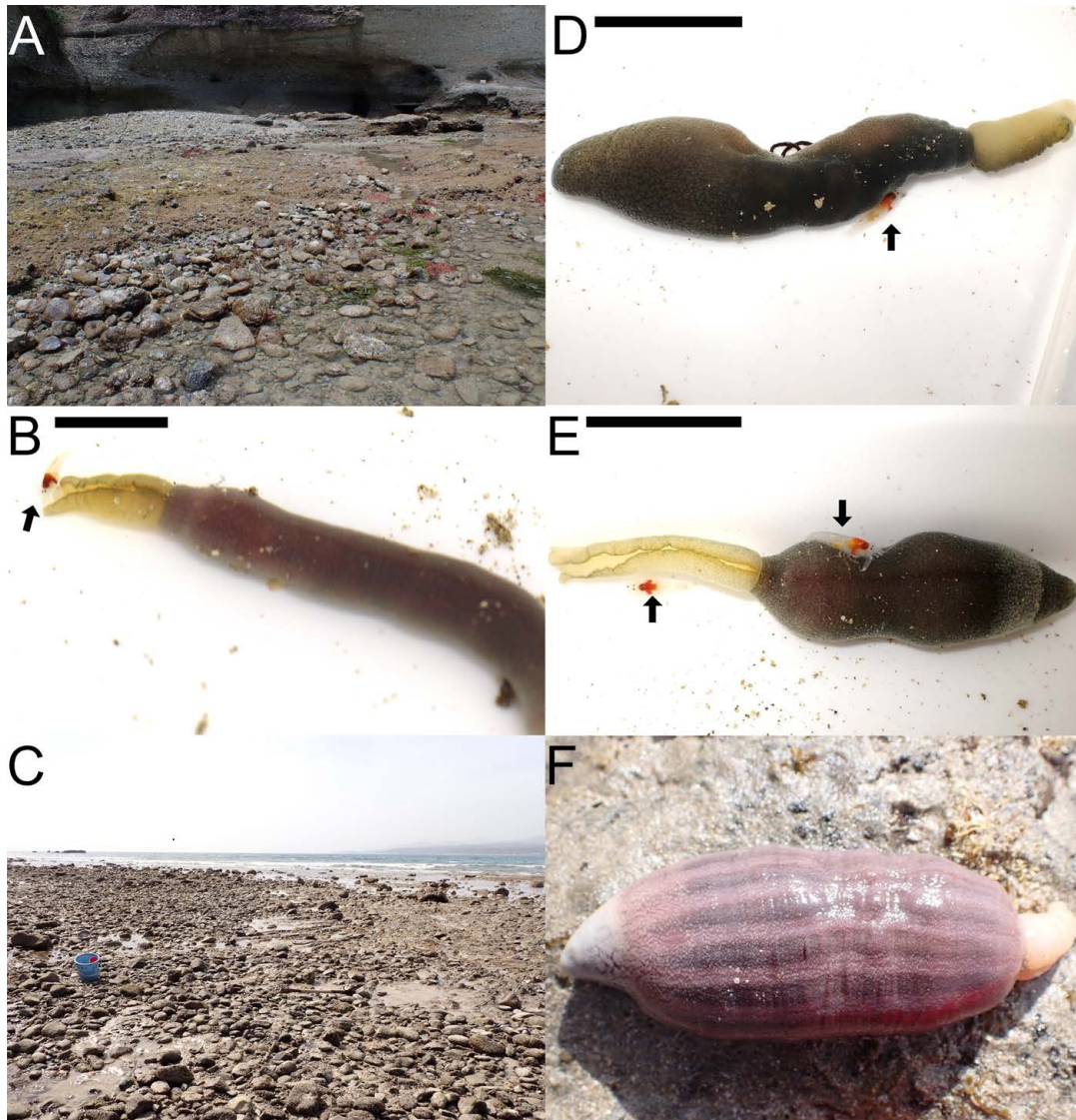


Fig. 2. (A) An intertidal flat at Banshozaki, Shirahama, southern Kii Peninsula. (B) *Athanopsis dentipes* dwelling near the *Anelassorhynchus* sp. 12 body (SMBL-V0878, male). (C) An intertidal flat at Kamiura, Kushimoto, southern Kii Peninsula. (D) *Athanopsis dentipes* dwelling near the *Anelassorhynchus* sp. 9 body (SMBL-V0875, ovigerous female). (E) Pair of *At. dentipes* (SMBL-V0876, male, SMBL-V0877, ovigerous female) dwelling near the *Anelassorhynchus* sp. 10 body. (F) *Listriolobus* cf. *sorbillans*, a host of *At. dentipes* (SMBL-V0874). Scale bars: 30 mm.

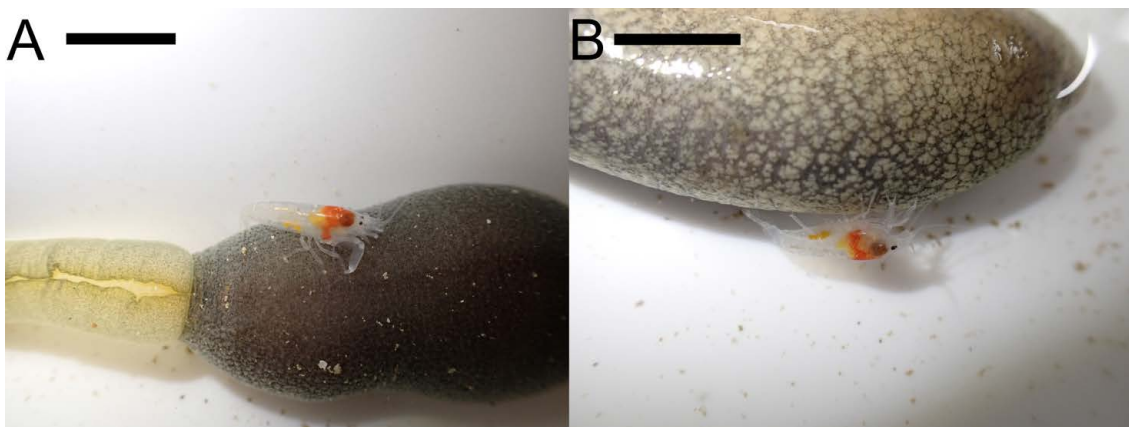


Fig. 3. (A) *Athanopsis dentipes* (SMBL-V0877, ovigerous female) scuttling over the body surface of the host *Anelassorhynchus* sp. 10. (B) *Athanopsis dentipes* (SMBL-V0875, ovigerous female) scuttling over the body surface of the host *Anelassorhynchus* sp. 9. Scale bars: 10 mm.

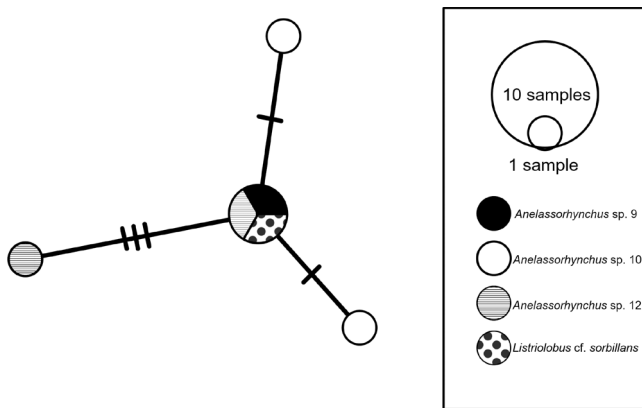


Fig. 4. Haplotype networks of *Athanopsis dentipes* based on COI sequences. Numbers in each circle (pie chart) indicate sample size, which is proportional to the host thalassematid of each pie diagram; *Anelassorhynchus* sp. 9, sp. 10, sp. 12, and *Listriolobus* cf. *sorbillans* are indicated by black, white, gray-striped, and dotted patterns, respectively. Small black nodes indicate hypothetical haplotypes.

et al. (2020). SMBL-V0874, ovigerous female, tl. 15.5 mm, cl. 6.0 mm, Kushimoto, Wakayama, Japan, 33°27'46" N, 135°46'34" E, coll. R. Goto, 31 March 2021, GenBank accession number: LC910707, host: *L. cf. sorbillans*. SMBL-V0875, ovigerous female, tl. 14.3 mm, cl. 5.1 mm, Kushimoto, Wakayama, Japan, 33°27'46" N, 135°46'34" E, coll. T. Sugiyama, 1 February 2023, GenBank accession number: LC910708, host: *An. sp. 9* sensu Goto et al. (2020). SMBL-V0876, male, tl. 14.7 mm, cl. 5.4 mm, Kushimoto, Wakayama, Japan, 33°27'46" N, 135°46'34" E, coll. T. Sugiyama, 3 February 2023, GenBank accession number: LC910709, host: *An. sp. 10* sensu Goto et al. (2020). SMBL-V0877, ovigerous female, tl. 14.4 mm, cl. 5.2 mm, Kushimoto, Wakayama, Japan, 33°27'46" N, 135°46'34" E, coll. T. Sugiyama, 3 February 2023, GenBank accession number: LC910710, host: *An. sp. 10* sensu Goto et al. (2020). SMBL-V0878, male, tl. 12.0 mm, cl. 4.6 mm, Shirahama, Wakayama, Japan, 33°41'40.9" N, 135°20'10.0" E, coll. T. Hanaoka, 28 May 2025, GenBank accession number: LC910711, host: *An. sp. 12* sensu Goto et al. (2020).

Description. Body not particularly compressed or depressed. Carapace (Fig. 6A, B) glabrous. Rostrum well developed, directed forward or weakly descending, narrowly triangular in dorsal view (about 1.1 times as long as wide at base), somewhat compressed laterally, overreaching distal margin of first article of antennular peduncle; tip rounded in lateral view; dorsal surface with a distinct dorsal carina running postward to the proximal 0.5 of the rostral length; ventral margin nearly straight; lateral margins faintly concave. Frontal margin with blunt orbital teeth (Fig. 6A, B) falling slightly short of distal corneal margin. Cardiac notch deep. Pterygostomial margin broadly rounded.

Pleon with sparse minute setae on dorsal surface; pleura all unarmed marginally. Sixth pleomere with movable plate at posteroventral corner. Telson (Fig. 6C) subrectangular about 1.5 times as long as anterior width: dorsal surface with two pairs of small spiniform setae submarginally, first pair located at 0.5 of telson length, second pair at 0.8 length; posterior margin gently convex, flanked by two robust lateral

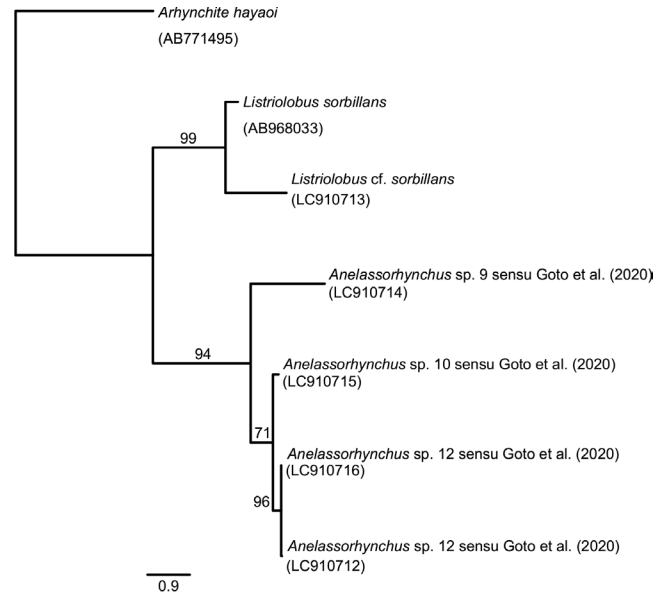


Fig. 5. Maximum likelihood tree of host thalassematids based on COI sequences. Species names are followed by their respective accession numbers. Numbers at nodes indicate bootstrap values.

spiniform setae at each posterolateral angle, bearing row of long setae.

Eye (Fig. 6A, B) partly exposed; cornea well pigmented, occupying most of terminal portion of eyestalk.

Antennular peduncle (Fig. 6A, B) stout. First article distinctly longer than wide in dorsal view, subequal in length to second article; armature of the ventromesial ridge produced anteriorly; stylocerite subacute distally, reaching 0.7 of second peduncular article.

Antenna (Fig. 6A, B) with stout basicerite having subacute tooth on ventrolateral distal angle. Carpocerite far overreaching antennular peduncle or scaphocerite.

Scaphocerite broad, about 2.0 times as long as wide, reaching antennular peduncle; lateral margin almost straight, distolateral tooth small, not reaching distal margin of lamella.

Third maxilliped (Fig. 6D) stout. Antepenultimate article noticeably broadened, with strongly convex dorsal margin, about 3.2 times as long as maximal width; penultimate article subrectangular, about 2.2 times as long as wide proximally; ultimate article furnished with transverse rows of thick serrulate setae, tapering distally, tip with two slender spiniform setae; arthrobranch absent (Fig. 6D). Exopod reaching distal margin of antepenultimate; distal corner subacute with some slender setae.

Chelipeds asymmetrical in shape and unequal in size; carried folded when not in use. Major cheliped of male (Fig. 7A–D) greatly enlarged, robust. Basis with a distodorsal spiniform seta. Ischium stout, with one distodorsal spiniform seta; mesial surface flattened, unarmed. Merus long, substantially inflated, widening distally, ventrally excavated to accommodate folded chela, ventrolateral and ventromesial margins strongly sinuous, particularly distal part of ventrolateral margin forming prominent, rounded expansion about 0.5 times as long as maximal width. Carpus short, cup-shaped, with broad blunt lobe ventromesially. Chela about 2.7 times as long as wide, surfaces almost smooth; palm

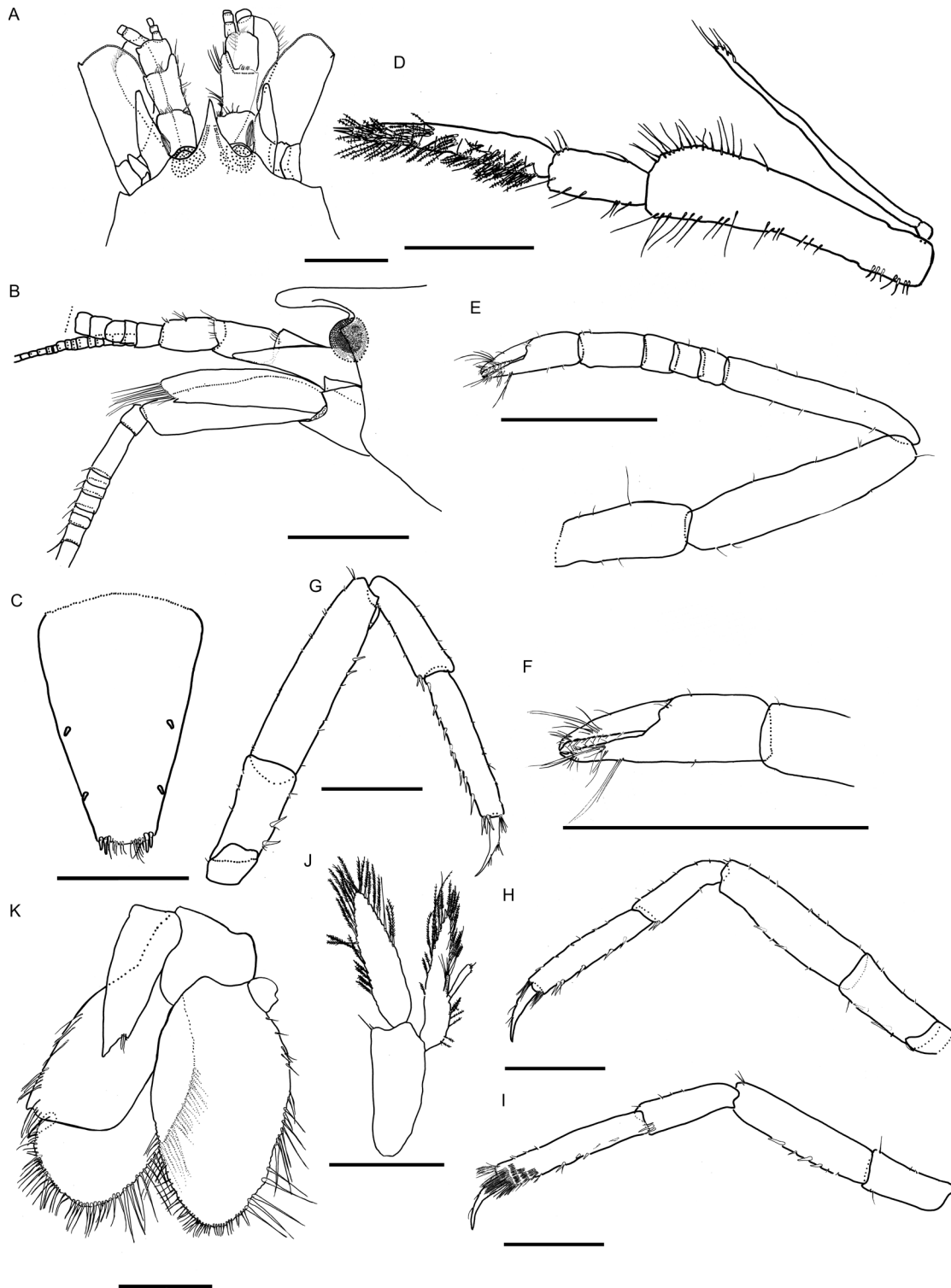


Fig. 6. *Athanopsis dentipes* (A–H) SMP-2198, male, cl. 6.1 mm, tl. 16.0 mm. (A) anterior part of carapace and cephalic appendage, dorsal view (flagella of antennae, and marginal setae of scaphocerite omitted); (B) anterior part of carapace and cephalic appendages, lateral view (flagella of antennae omitted); (C) telson, dorsal view; (D) left third maxilliped lateral view (coxa omitted); (E) left second pereopod, lateral view; (F) same, chela, lateral view; (G) right third pereopod, lateral view; (H) left fourth pereopod, lateral view; (I) right fifth pereopod, mesial view; (J) right second pleopod, dorsal view, (K) left uropods, dorsal view. Scale bars: 1.0 mm.

strongly swollen, ovoid in outline, about 1.9 times as long as wide, no depression on surfaces; fingers not gaping when closed; pollex deflexed, forming deep notch at base, about

0.5 times as long as palm; cutting edge of pollex with a large, blunt tooth on proximal half. Dactylus slightly longer than pollex, about 0.7 times as long as palm, gently curved, terminat-

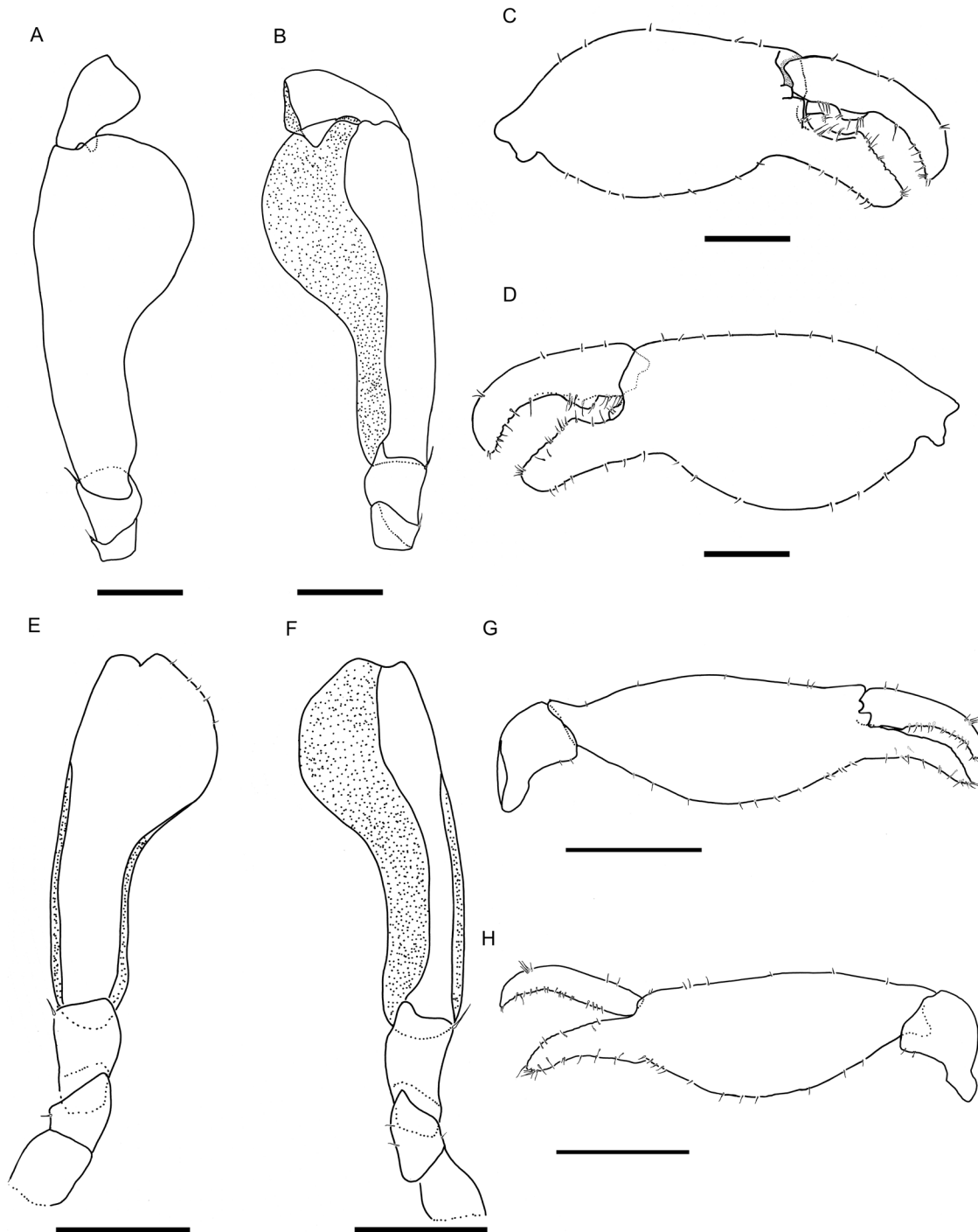


Fig. 7. *Athanopsis dentipes* [(A–D) SMP-2198, male, cl. 6.1 mm, tl. 16.0 mm; (E–H) SMBL-V0878, male, cl. 4.6 mm, tl. 12.0 mm). (A) right major cheliped, coxa to carpus, lateral view; (B) same, mesial view; (C) same, chela, dorsolateral view; (D) same, ventromedial view; (E) right minor cheliped, coxa to merus, lateral view; (F) same, mesial view; (G) right minor cheliped, chela, dorsolateral view; (H) same, ventromesial view. Scale bars: 1.0 mm.

ing in blunt apex; cutting edge of dactylus with one large, blunt tooth located at proximally 0.4 area, multidenticulate distally.

Minor cheliped of male (Fig. 7E–H) shorter and slenderer than major cheliped. Ventrolateral expansion of merus about 0.4 times as long as maximal width; chela about 3.3 times as long as wide; palm moderately swollen, about 2.4 times as long as wide and dactylus length; fingers not

gaping when closed, tips not crossing, cutting edge of dactylus without conspicuous tooth.

Major cheliped of female (Fig. 9A–D) similar to minor cheliped of male. Ventrolateral expansion of merus about 0.4 times as long as maximal width and less pronounced than in male. Palm about 2.4 times as long as wide. Teeth at the occlusal margin much less developed than in male.

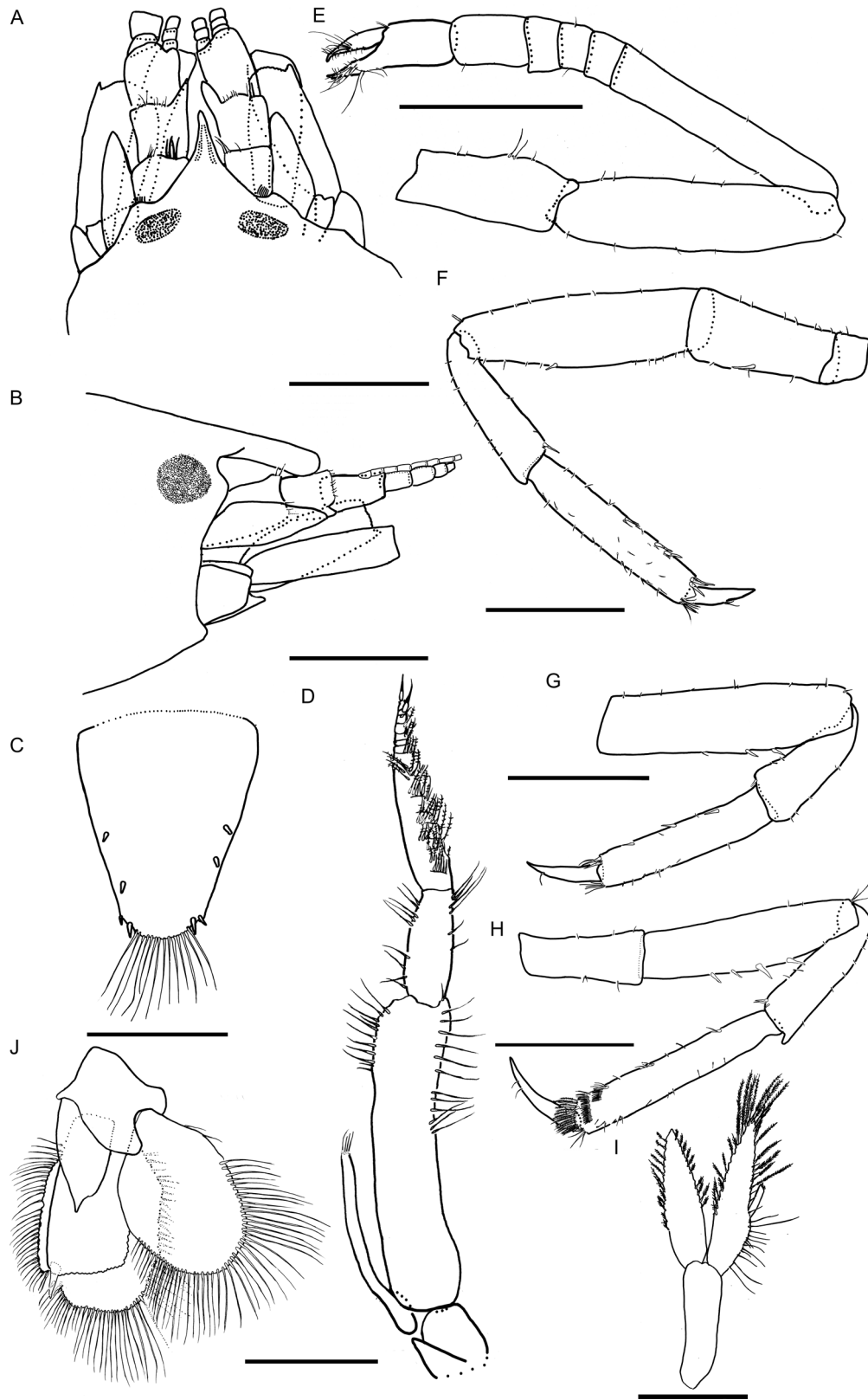


Fig. 8. *Athanopsis dentipes* (SMBL-V0874, female, cl. 6.0 mm, tl. 15.5 mm). **(A)** Frontal margin of carapace and cephalic appendages (antennular flagellum, left antenna flagellum, right antenna and setae on scaphocerite omitted), dorsal view (flagella of antennae, peduncle of right antenna, and marginal setae of scaphocerite omitted); **(B)** frontal margin of carapace and frontal appendages, lateral view (flagella of antennae omitted); **(C)** telson, dorsal view; **(D)** left third maxilliped, lateral view; **(E)** left second pereopod, lateral view; **(F)** left third pereopod, lateral view; **(G)** right fourth pereopod, lateral view (basis and ischium omitted); **(H)** right fifth pereopod, lateral view; **(I)** right second pleopod, dorsal view; **(J)** left uropods, dorsal view. Scale bars: 1.0 mm.

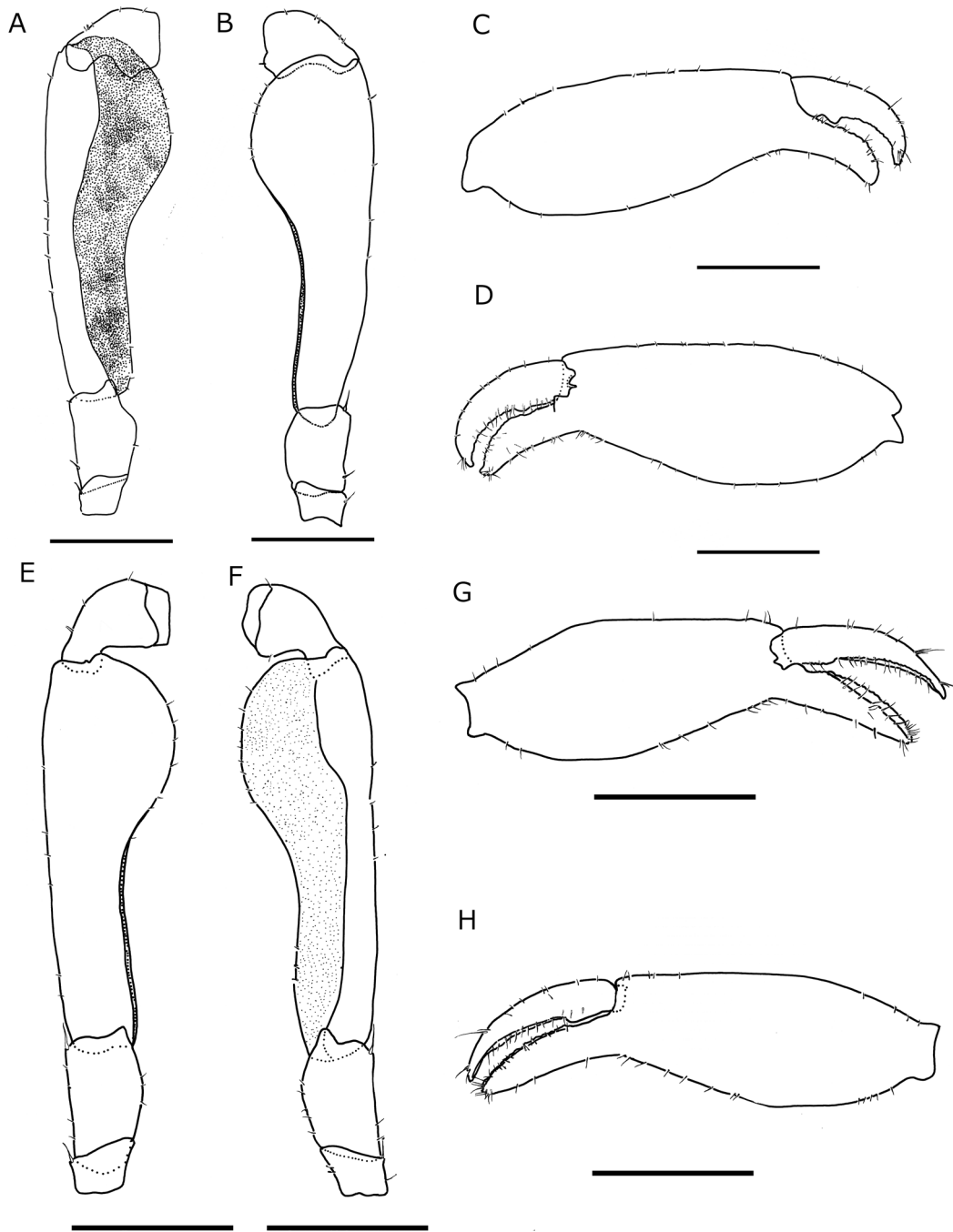


Fig. 9. *Athanopsis dentipes* (SMBL-V0874, female, cl. 6.0 mm, tl. 15.5 mm). **(A)** left major chela, coxa to carpus, medial view; **(B)** same, lateral view; **(C)** left major chela, palm to finger, ventromedial view; **(D)** same, dorsolateral view; **(E)** right minor chela, coxa to carpus, lateral view; **(F)** same, medial view; **(G)** right minor chela to finger, dorsolateral view; **(H)** same, ventromedial view. Scale bars: 1.0 mm.

Dactylus subequal in length to palm.

Minor cheliped of female (Fig. 9E–H) shorter and slenderer than major cheliped. Ventrolateral expansion of merus about 0.3 times as long as maximal width and less pronounced than in male. Palm about 2.5 times as long as wide. Dactylus subequal in length to palm.

Second pereopod (Fig. 6E, F) slender, overreaching distal end of antennal carpocerite by length of chela. Ischium about 0.6 times as long as merus; carpus divided into five articles, with approximate ratio 1.0: 0.1: 0.2: 0.2: 0.3; chela

about 0.3 times as long as carpus, fingers as long as palm.

Third pereopod (Fig. 6G) rather stout; ischium with two spiniform setae on ventroproximal margin; merus about 4.0 times as long as wide, ventrolateral distal angle with small tooth, ventral margin with two spiniform setae distal to mid-length; carpus slightly widened distally, about 2.8 times as long as distal width, flexor distal margin with one pair of spiniform setae; propodus about 5.4 times as long as wide, flexor margin with eight strong spiniform setae and three spiniform setae on flexor distal margin; dactylus simple, about 0.4 times

as long as propodus, slightly curved, extensor margin with one tiny and one spiniform setae located at midlength.

Fourth pereopod (Fig. 6H) similar to third pereopod, but slightly shorter; propodus with five strong spiniform setae on flexor margin, flexor distal margin with dense slender setae; dactylus with sparse short setae.

Fifth pereopod (Fig. 6I) slightly shorter than fourth pereopod; ischium unarmed; merus with four spiniform setae on ventral margin; propodus with three spiniform setae on flexor margin and four transverse rows of brush-like stiff setae, constituting grooming apparatus, located at distal one-fourth.

Male second pleopod (Fig. 6J) with appendix masculina being about half-length of the appendix interna, apex with tuft of simple setae.

Uropod (Fig. 6K) with lateral lobe of protopod bearing large, subacute lateral tooth and smaller but distinct acute mesial tooth adjacent to lateral tooth; exopod with diaeresis straight, curving mesially; distolateral tooth small, blunt,

adjacent distolateral spiniform seta; endopod ovoid, as long as exopod.

Coloration in life. Body whitish translucent; large bright-red patch extending from dorsomedial carapace to lateral sides; dorsal patch larger than lateral patches; eggs yellow in non-eye stage.

Size range. Male—carapace length 4.6–6.1 mm, total length 12–16 mm; Female—carapace length 5.2–6.0 mm, total length 14.2–15.5 mm.

Distribution. Only known from Japan: Nomo Bay, Nagasaki Prefecture (holotype) and Amakusa, Kumamoto Prefecture (paratype) in western Kyushu Island (Miya, 1980); Shirahama and Kushimoto, Wakayama Prefecture, southern Kii Peninsula, central Japan (this study) (Fig. 1).

Reproduction. Reproductive activity of this shrimp was observed in spring. In this survey, three ovigerous females were collected in March 2021 and February 2023 (Table 2, Fig. 10D–F). Of these, only a female shrimp collected on 3



Fig. 10. Color patterns in life of *Athanopsis dentipes*. (A–C) SMBL-V0878, male, cl. 4.0 mm, tl. 12.0 mm; (D–F) SMBL-V0874, ovigerous female, cl. 6.0 mm, tl. 15.5 mm. Scale bars: 3.0 mm.

February 2023 (SMBL-V0877) formed a pair with a male (SMBL-V0876).

Identity of host worms. Figure 5 shows the ML tree of the host thalassematids plus *L. sorbillans*. *Listriolobus* cf. *sorbillans* (Lampert, 1883) was morphologically identical with *L. sorbillans* in the number of gonoducts and trunk muscular arrangements. However, there were 20.6% K2P genetic differences between our specimens and *L. sorbillans* from the Ryukyu Archipelago, suggesting that they are different species. The host thalassematids of *Anelassorhynchus* spp. were genetically separated into three species, each completely or nearly completely matching *An. sp. 9*, *sp. 10*, and *sp. 12* sensu Goto et al. (2020).

Host associations. Separation trials were conducted to observe host-seeking behavior of *At. dentipes* and *Al. barbatus*. After being removed and placed apart from the host thalassematids, shrimps sought and returned to the host, although some behaviors were different between the two species. *Athanopsis dentipes* tended to scuttle over the body surface of their host and sometimes hide themselves in crevices beneath the body surface of the thalassematid. In contrast, *Al. barbatus* did not show such behaviors but exhibited a hiding behavior. They frequently moved their pleopods and uropods to hide themselves under their host.

Co-occurring thalassematid associates. Specimens of *At. dentipes* were collected together with the commensal bivalve *Borniopsis yamakawai* (Yokoyama, 1922) from the same burrow of *L. cf. sorbillans* in Kamiura Beach. *Anelassorhynchus* spp. 9 and 12 have also recently been recorded as hosts of the ectocommensal bivalve *Sagamiscintilla thalassemicola* (Habe, 1962) (Goto and Ishikawa, 2019; Goto et al., 2023); notably, *Anelassorhynchus* sp. 9 was likewise collected from Kamiura Beach. *Alpheus barbatus* was also collected from the burrows of *Anelassorhynchus* spp. 10 and 12 in Kushimoto and Shirahama, respectively, although *At. dentipes* and *Al. barbatus* were never collected together from the same host burrow.

Remarks. Our specimens collected from Wakayama Prefecture were clearly identified with *At. dentipes* because of the following diagnostic features (Miya, 1980): (1) a ventrally straight rostrum in lateral view; (2) the presence of orbital teeth; (3) a large tooth on the cutting edge of the dactylus of the major chela; (4) a spiniform seta on the ventral margin of the merus of the third pereopod; (5) a small sub-acute tooth at the ventrolateral distal angle of the merus of the third pereopod.

Athanopsis dentipes is morphologically closest to *At. australis* described from eastern Australia (Banner and Banner, 1982; Anker and Ah Yong, 2007), although, in the original description, Banner and Banner (1982) did not mention *At. dentipes*. They share the following diagnostic characters: (1) third pereopod merus having one–three spiniform seta(e) ventrally; (2) eyes partly exposed in dorsal and lateral views.

Athanopsis dentipes can be distinguished from *At. australis* by the following characters: (1) the rostrum of *At. dentipes* is ventrally straight in the lateral view (Miya, 1980, fig. 1; this study, Figs. 6B, 8B), but that of *At. australis* is ventrally concave (Banner and Banner, 1982, fig. 1b; Anker and Ah Yong, 2007, fig. 1b); (2) a large tooth on the cutting



Fig. 11. *Arete dorsalis* (HMNH-C527), body, left lateral view, left chela, lateral view, and right chela, ventromedial view. Scale bar: 5.0 mm.

edge is present in the male of *At. dentipes* (Miya, 1980, fig. 2B; this study, Figs. 7C, 9D), but such a tooth is absent in *At. australis* (Anker and Ah Yong, 2007, fig. 1f); (3) the merus of the third pereopod has a small distal tooth at the ventrolateral angle in *At. dentipes* (Miya, 1980, fig. 1; this study, Figs. 6G, 8F), whereas such a tooth is absent in *At. australis* (Banner and Banner, 1982, fig. 1b; Anker and Ah Yong, 2007, fig. 1h).

Athanopsis dentipes can be easily separated from *At. brevirostris*, *At. dawa*, *At. gotoi*, *At. platyrhynchus*, *At. saurus*, and *At. tarahomii* by the presence of one–three stout spiniform seta(e) on the third pereopod merus. In the latter six species, the third pereopod merus is devoid of spiniform setae on the ventral margin (Coutière, 1897; Miya, 1980, 1984; Banner and Banner, 1981, 1982; Anker, 2011, 2012, 2023; Marin et al., 2014). Furthermore, *At. dentipes* can be separated from *At. rubricincta* by the presence of orbital teeth, which are absent in *At. rubricincta* (Berggren, 1991).

Yoshigou and Nakamura (2005) recorded *At. dentipes* from Okinawa Island, the Ryukyu Islands. We examined the voucher specimen (HMNH-C527) to verify the identity (Fig. 11). Our reexamination has revealed that the specimen actually represents *Arete dorsalis* (Stimpson, 1860), of which the identification was based on the following traits: rostrum slender with acute tip; orbital teeth absent; pterygostomial angle of carapace rounded; sixth pleomere without movable plate at posteroventral angle; distolateral margin of palm of cheliped at base of dactylus obtuse; carpus of second pereopod with four subarticles; epipod absent on third pereopod (Bruce, 1986; Hayashi, 1995; Anker and Jeng, 2007; Anker, 2025).

DISCUSSION

In the present study, we report the first record of *At. dentipes* since its original description 45 years ago. The delay in its rediscovery can be attributed to several factors. Notably, the symbiotic fauna of thalassematid burrows on temperate Japanese rocky shores has remained understudied. Moreover, the sparse distribution of thalassematid populations in these regions decreases the probability of detection. In spite of the recent activity in sampling of thalas-

sematids in the subtropical Ryukyu Islands (e.g., Goto et al., 2011, 2024; Goto and Kato, 2012; Goto, 2017), no specimens attributable to *At. dentipes* have been encountered. The currently available data would suggest that *At. dentipes* might be restricted to warm temperate waters.

In his original description of *At. dentipes*, Miya (1980) identified the host worm of *At. dentipes* with *Anelassorhynchus* cf. *mucosus* (as *Thalassema ?mucosa*), but later Miya (1995) stated the host worm of *At. dentipes* as *Urechis unicinctus* (Urechidae). In this study, association between *At. dentipes* and the four thalassematid species, *An. sp. 9*, *sp. 10*, and *sp. 12* sensu Goto et al. (2020) and *L. cf. sorbillans* is documented. Furthermore, as reviewed above, association between species of *Athanopsis* and thalassematid worms has been reported. It is reasonable to assume that Miya (1995)'s description of the host worm was incorrect.

Previous studies have typically recorded each species of *At. dentipes* from a single species of thalassematid belonging to Thalassematini. In contrast, this study recorded *At. dentipes* from two genera and four species of Thalassematini. This observation suggests that *At. dentipes* is associated with a relatively wide host range across Thalassematini. Additionally, according to the result of haplotype network analysis, there is no clear genetic differentiation among the shrimps on different host species.

In previous studies, species of *Anelassorhynchus* have been recorded as hosts in three species of *Athanopsis* (i.e., *At. dentipes*, *At. australis*, and *At. gotoi*) collected from the Indo–West Pacific Ocean. Furthermore, while *At. saurus* from New Caledonia was reported to be associated with what is probably *Ochetostoma* sp. (Anker, 2023), the host is identifiable as a member of *Anelassorhynchus* based on the figure (Anker, 2023, fig. 9). This identification is supported by the absence of longitudinal muscle bands and the lack of fasciculation. Therefore, *Anelassorhynchus*–*Athanopsis* associations have been widely observed throughout the Indo–West Pacific.

Conversely, *Listriolobus* was first recorded as hosts of *Athanopsis* in this study. Anker (2023) identified the host thalassematid of *At. brevirostris* as *Ochetostoma* sp. or *Listriolobus* sp. However, the host worm reported by Anker (2023, fig. 8) shows characteristic fasciculated longitudinal muscle bands, suggesting that it represents a species of *Ochetostoma*, although definite identification is not possible.

Anker and Ah Yong (2007) conducted a preliminary phylogenetic analysis of *Athanopsis* based on morphological characters, which recovered two major clades: one comprising *At. brevirostris* and *At. rubricincta*, and the other comprising *At. australis*, *At. dentipes*, and *At. platyrhynchus*. Within the latter clade, *At. dentipes* was sister to *At. australis*. *Athanopsis australis* is known to be associated with *An. porcellus* in Australia (Edmunds et al., 2012). Because *At. dentipes* also exploits hosts of the genus *Anelassorhynchus* and has a relatively broad host range, their divergence is unlikely to have been driven by host switching. Instead, speciation between *At. australis* and *At. dentipes* was more plausibly promoted by geographic isolation or environmental differentiation, such as latitudinal or thermal gradients.

Our findings have important implications for the understanding of host–symbiont relationships as well as for the conservation of *At. dentipes*. It is important to conserve the

habitats of thalassematids and their symbiotic fauna due to their restricted distribution, rarity, and specialization. Consequently, several species have been recognized as endangered species in Japan (e.g., Japanese Association of Benthology, 2012; Ministry of the Environment Japan, 2017a, b). Within the genus *Athanopsis*, *At. australis* is categorized as an endangered species in the state of Victoria, Australia. Conservation measures for the species have also been proposed in this area (Department of Environment, Land, Water and Planning, 2021; Edmunds et al., 2012). Our results suggest that *At. dentipes* utilizes an uncommon habitat, making the species particularly vulnerable to extinction. Accordingly, conservation strategies for *At. dentipes* should be developed following detailed assessments of host distribution, burrow density, and environmental stability.

In recent years, several alpheid shrimps associated with thalassematids have been described in Japanese waters (Nomura, 2000; Anker, 2012; Anker et al., 2015; Komai, 2015). Comprehensive surveys of thalassematid burrow fauna are therefore likely to reveal a substantial undocumented diversity of symbiotic alpheids, further emphasizing the conservation importance of these cryptic benthic habitats.

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COMPETING INTERESTS

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

TH designed the study, conducted field sampling, collected data, and drafted the manuscript. IH contributed to specimen collection and identification, and reviewed and edited the draft. ST conducted field sampling, collected data, and reviewed and edited the draft. KN provided specimens and reviewed and edited the draft. GI reviewed and edited the draft. MS reviewed and edited the draft and supervised the study. RG designed and supervised the study, conducted field sampling, collected data, performed genetic analyses, and drafted the manuscript. All authors read and approved the final version of the manuscript.

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