A new species of *Alvinocaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vents in the Izu-Bonin and Mariana Arcs, north-western Pacific

Retori Hiraoka[1] [ID], Tomoyuki Komai[2] and Shinji Tsuchida[3]

[1]Marine Biological Research Institute of Japan Co., Ltd, 4-3-16 Yutakacho, Shinagawa, Tokyo 142-0042, Japan; [2]Natural History Museum and Institute, 955-2 Aoba-cho, Chuo-ku, Chiba 260-8682, Japan and [3]Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

Abstract

A new species of the caridean genus *Alvinocaris*, *A. marimonte* sp. nov., is described and illustrated on the basis of specimens collected from hydrothermal vents at three locations in Izu-Bonin and Mariana Arcs of the north-western Pacific Ocean, Myojin Knoll (1224 m depth), NW Eifuku (1574–1582 m depth) and NW Rota seamounts (525 m depth). It is the 17th species assigned to *Alvinocaris*, and differs from all other congeneric species in several morphological characteristics derived from the rostrum length and armature, the carapace armature, the shape of the posterior margin of the telson and the armature of the third and fourth pereopods. Results of molecular phylogenetic analyses based on partial sequences of the mitochondrial COI and nuclear ITS-I genes compared between specimens of *A. marimonte* sp. nov. and other known species of *Alvinocaris* supported our recognition of the new species, although available data are still limited. *Alvinocaris marimonte* sp. nov. is represented by two morphotypes, distinguished by the armature of the posterior margin of the telson (spines *vs* plumose setae), which were not detected as separate species by the molecular analysis. Our discovery of the intraspecific variation in the armature of the posterior margin of the telson led us to reassess diagnostic characters used to distinguish species within the genus *Alvinocaris*.

Introduction

The caridean family Alvinocarididae is endemic to chemosynthetic environments in deep water (252–4960 m depth), and is currently represented by 36 species in nine genera, *Alvinocaridinides* Komai & Chan, 2010, *Alvinocaris* Williams & Chace, 1982, *Keldyshicaris* Vereshchaka, Kulagin & Lunina, 2015, *Manuscaris* Komai & Tsuchida, 2015, *Mirocaris* Vereshchaka, 1997, *Nautilocaris* Komai & Segonzac, 2004, *Opaepele* Williams & Dobbs, 1995, *Rimicaris* Williams & Rona, 1986, and *Shinkaicaris* Komai & Segonzac, 2005 (Komai & Tsuchida, 2015; Vereshchaka *et al.*, 2015; Komai *et al.*, 2016; Wang & Sha, 2016, 2017; Martin *et al.*, 2018; Komai & Giguère, 2019). Vereshchaka *et al.* (2015) proposed to recognize three subfamilies to reflect the phylogenetic pattern inferred by them, Alvinocaridinae (*Alvinocaris*), Mirocaridinae (*Mirocaris* and *Nautilocaris*) and Rimicaridinae (*Alvinocaridinides*, *Manuscaris*, *Opaepele*, *Rimicaris* and *Shinkaicaris*). *Alvinocaris*, which contains 16 species from the Atlantic, Pacific and Indian Oceans (Martin *et al.*, 2018) is the most speciose genus of Alvinocarididae, and the discovery of new species is still continuing. These include: *A. alexander* Ahyong, 2009, *A. brevitelsonis* Kikuchi & Hashimoto, 2000, *A. chelys* Komai & Chan, 2010, *A. costaricensis* Martin, Wall, Shank, Cha, Seid & Rouse, 2018, *A. dissimilis* Komai & Segonzac, 2005, *A. komaii* Zelnio & Houdez, 2009, *A. longirostris* Kikuchi & Ohta, 1995, *A. lusca* Williams & Chace, 1982 (type species), *A. markensis* Williams, 1988, *A. kexueae* Wang & Sha, 2017, *A. methanophila* Komai, Shank & Van Dover, 2005, *A. muricola* Williams, 1988, *A. niwa* Webber, 2004, *A. solitaire* Yahagi, Watanabe, Kojima, Beedessee & Komai, 2014, *A. stactophila* Williams, 1988 and *A. williamsi* Shank & Martin, 2003. Four of these 16 species are known from the north-western Pacific: *A. brevitelsonis*, known only from hydrothermal vent on Minami-Ensei Knoll, Okinawa Trough and NW Eifuku Seamount in the Marian Arc (Komai & Segonzac, 2005; Tsuchida *et al.*, 2012; Yahagi *et al.*, 2015); *A. chelys*, known only from hydrothermal vents offshore north-eastern Taiwan (Komai & Chan, 2010); *A. dissimilis*, known only from hydrothermal vents on Minami-Ensei Knoll (Komai & Segonzac, 2005; Yahagi *et al.*, 2015), and *A. longirostris*, known from hydrothermal vents of the Okinawa Trough and cold seep sites in Sagami Bay, Japan, and in the South China Sea (Komai & Segonzac, 2005; Li, 2015; Yahagi *et al.*, 2015).

In this study, we describe a new species of *Alvinocaris*, *A. marimonte* sp. nov., from the Izu-Bonin and Mariana Arcs, on the basis of specimens collected from the Myojin Knoll in the Izu-Bonin Arc, and the NW Eifuku and NW Rota Seamounts in the Mariana Arc, at depths of 525–1580 m. Our identification of this new species is supported by both morphological comparisons and molecular genetic analyses based on partial sequences of

mitochondrial COI and nuclear ITS-I genes. The new species that we report here represents the 17th species of the genus *Alvinocaris*.

Materials and methods

Specimens collection

Specimens were collected over the course of three dives of ROV 'Hyper-Dolphin' (RV 'Natsuhima'): #1493 (16 March 2013) at Myojin Knoll (32°06.2′N 139°53.1′E, 1224 m depth); #492 (27 October 2005), #494 (29 October 2005) at NW Eifuku Seamount (21°29.2N 144°02.5′E, 1574–1582 m depth); and #1161 (26 July 2010) at NW Rota Seamount (14°36.0′N 144°46.5′E, 525 m depth) (Figure 1). Specimens were collected using a slurp gun and multiple canister bottles loaded on the ROV 'Hyper-Dolphin', and preserved in either 75 or 99.5% ethanol. Postorbital carapace length (CL) was used as a measurement of the size of specimens, and the morphological terminology employed in species description generally follows Komai & Segonzac (2005).

Genetic analyses

For the genetic analyses, seven specimens (two from Myojin Knoll, four from NW Eifuku Seamount, and one from NW Rota Seamount) were used.

DNA was extracted from the pleon muscle using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). The partial sequences of the mitochondrial cytochrome oxidase subunit I (COI), and of the nuclear intergenic spacer region I (ITS-I) were amplified through polymerase chain reactions (PCR), using Ex Taq polymerase (TAKARA, Tokyo, Japan), with the universal primers LCO1490 (GGT CAA CAA ATC ATA AAG ATA TTG G; Folmer et al., 1994) and HCO2198 (TAA ACT TCA GGG TGA CCA AAA AAT CA; Folmer et al., 1994) for COI, and SP-1–3′ (ATT TAG CTG CGG TCT TCA TC; Chu et al., 2001) and SP-1–5′ 138 (CAC ACC GCC CGT CGC TAC TA; Chu et al., 2001) for ITS-1.

The amplification mixture (25 μl) contained 2.5 μl of 10× buffer reagent (100 mM Tris-HCl with a pH of 8.3, 500 mM KCL and 15 mM $MgCl_2$ bovine serum albumin), 2.0 μl of dNTP, 1.0 μl of each of the primers, 0.125 μl of Taq DNA polymerase, 1.0 μl of template DNA, and sterile H_2O to make up the balance volume. Thermal cycling conditions were 96.0 °C for 60 s, followed by 35 cycles of 96.0 °C for 30 s/48.0 °C for 30 s/72.0 °C for 60 s, and a final extension of 72.0 °C for 7 min. Sequencing was conducted using an ABI PRISM 3130xl Genetic Analyzer (Applied Biosystems Japan Ltd, Tokyo, Japan). The sequence strands for each gene were proofread and assembled using Codon Code Aligner version 3.7 (Codon Code Corporation, Dedham, MA, USA). In order to estimate the degree of similarity between the sequences of our specimens and other sequences deposited in GenBank, partial sequences of both genes were compared using the gapped BLAST search algorithm.

Maximum-likelihood (ML) and Neighbour-joining (NJ) trees using COI sequences were constructed with 11 species of *Alvinocaris*, and with *Mirocaris fortunata* (Martin & Christiansen, 1995) as an outgroup, using MEGA7 (Kumar et al., 2016). The nucleotide divergences of COI and ITS-I were calculated based on the Kimura two-parameter (K2P) distance model (Kimura, 1980). Bootstrap values, for both ML and Neighbour-joining (NJ), were calculated from 1000 iterations.

The GenBank accession numbers for the partial sequences examined in this study are LC481565–LC481570, AB779505 (for COI) and LC481899–LC481904, AB914466 (for ITS-I).
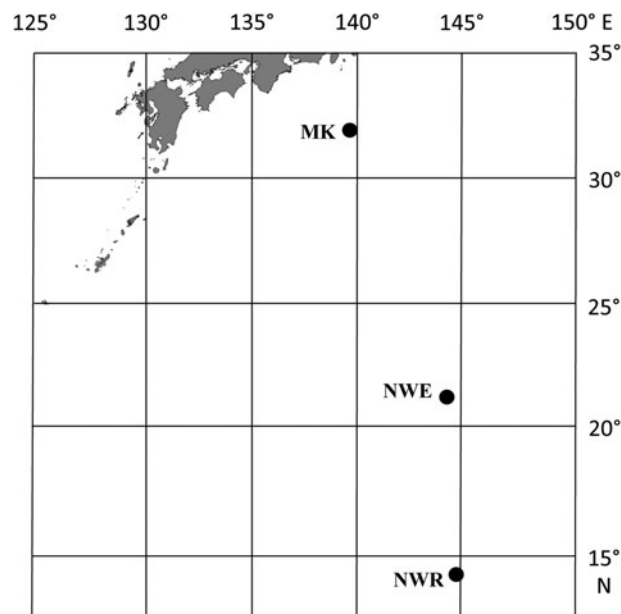

Fig. 1. Map showing collection sites in the Izu-Bonin and Mariana Arcs in the North-west Pacific. Solid circles showed the hydrothermal vent fields: MK, Myojin Knoll; NWE, North-west Eifuku Seamount; NWR, North-west Rota Seamount.

Results

Species description

Systematic

Order DECAPODA Latreille, 1802
Infraorder CARIDEA Dana, 1852
Family ALVINOCARIDIDAE Christoffersen, 1986
Genus *Alvinocaris* Williams & Chace, 1982
Alvinocaris marimonte sp. nov.
(Figures 2–7)

Alvinocaris brevitelsonis—Tsuchida et al., 2012: 188, figure 11.15
Alvinocaris sp. —Yahagi et al., 2015

Type material

Holotype: female, CL 9.5 mm, Myojin Knoll, Izu-Bonin Arc, 32°06.2′N 139°53.1′E, 1224 m depth ROV 'Hyper-Dolphin' #1493, 16 March 2013 (JAMSTEC 1130036387), GenBank accession numbers LC481565 (for COI) and LC481899 (for ITS-I).

Paratypes: one female, CL 9.0 mm, same data as holotype (JAMSTEC 1130041225), GenBank accession numbers LC481566 (for COI) and LC481900 (for ITS-I). Two males, CL 6.0, 6.8 mm, four females, CL 7.0–10.1 mm, one ovigerous female, CL 12.0 mm, NW Eifuku Seamount, Mariana Arc, 21°29.2′N 144°02.5′E, 1582 m depth, ROV 'Hyper-Dolphin' #494, 29 October 2005 (JAMSTEC 2050041226–2050041232). One female CL 7.2 mm, NW Rota Seamount, Mariana Arc, 14°36.0′N 144°46.5′E, 525 m depth, ROV 'Hyper-Dolphin' #1161, 26 July 2010 (JAMSTEC 1100023686). Accession numbers AB779505 (for COI) and AB914473 (for ITS-I).

Non-type: three females, CL 10.0–10.1 mm, one ovigerous female, CL 10.2 mm, NW Eifuku Seamount, Mariana Arc, 21°29.2′N 144°02.5′E, 1574 m depth, ROV 'Hyper-Dolphin' #492, 27 October 2005 (JAMSTEC061133–061136), GenBank accession numbers LC481567– LC481565 (for COI) and LC481901–LC481904 (for ITS-I).

Description. Body (Figure 2) moderately robust; integument thin and soft, but not membranous. Rostrum (Figures 3A, C & 7A, D) slightly descending or directed forward, reaching mid-
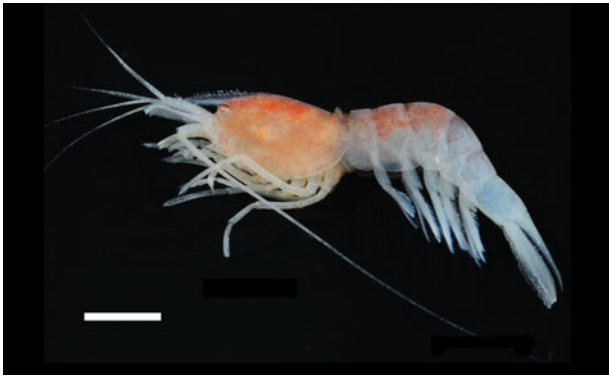
Fig. 2. *Alvinocaris marimonte* sp. nov., paratype, female (CL 7.0 mm), JAMSTEC 2050041227, entire animal in lateral view. Scale bar = 5.0 mm.
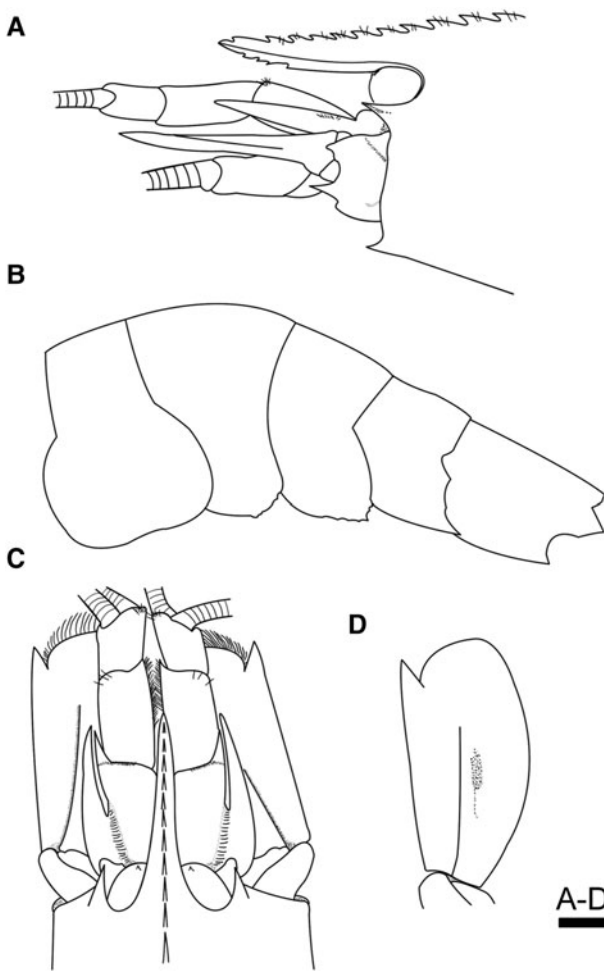

Fig. 3. *Alvinocaris marimonte* sp. nov., holotype, female (CL 9.5 mm), JAMSTEC 1130036387: (A) anterior part of carapace and cephalic appendages, lateral view; (B) same, dorsal view; (C) second to sixth pleomeres, lateral view; (D) left antennal scale, dorsal view (marginal setae omitted). Scale bars = 1 mm.
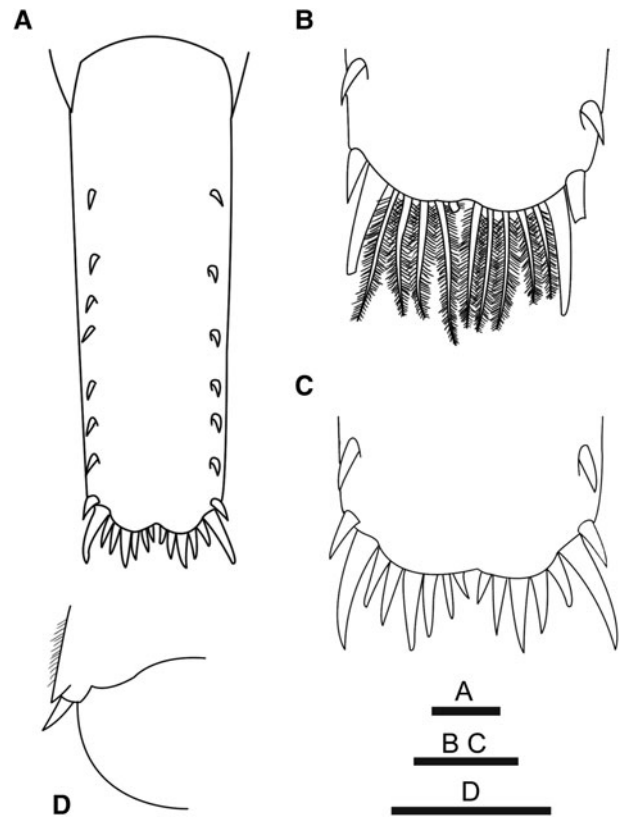

Fig. 4. *Alvinocaris marimonte* sp. nov. A, C, holotype female (CL 9.5 mm), JAMSTEC 1130036387, B, paratype, female (CL 7.0 mm), JAMSTEC 2050041227: (A) telson, dorsal view; (B, C) posterior margin of telson, dorsal view; (D) posterolateral part of left uropodal exopod, dorsal view. Scale bars = 1 mm.

length to distal margin of second article of antennular peduncle (0.38–0.60 times as long as carapace); dorsal margin armed with 13–17 moderately small teeth, including 5–7 postrostral teeth, posterior-most tooth arising at 0.23–0.39 of carapace length; ventral margin with 0–4 small teeth; ventrolateral margin sharply carinate, merging into orbital margin. Carapace (Figures 3A, C & 7A, C) 1.1–1.5 times longer than wide; postrostral median ridge moderately high, sloping anteriorly to rostrum;

dorsal angle 160–165°; antennal tooth moderately strong, acuminate; pterygostomial tooth moderately produced anteriorly, extending as far as or slightly beyond antennal tooth; anterolateral margin between antennal and pterygostomial teeth concave; postantennal groove shallow; branchial region moderately convex.

Pleon (Figure 3B) rounded dorsally; pleura of anterior 2 pleomeres broadly rounded; third pleuron with 0–8 minute marginal teeth, fourth pleuron with 4–8 minute marginal teeth posteriorly; fifth pleuron with 1 strong posteroventral tooth and 1–3 additional teeth on posterolateral margin; sixth pleomere 1.20–1.53 times longer than high.

Telson (Figure 5A) not reaching posterior margin of uropodal endopod, with lateral margins almost parallel; length 2.73–3.18 times anterior width and 4.25–5.25 times posterior width; armed with 6–8 dorsolateral spines, arranged in linear row, on either side; posterior margin (Figure 4B, C) usually weakly bilobed with shallow median notch, armed with 2 lateral unequal spines (inner pair longer than outer pair), and with row of 10–11 spines and 0–2 median plumose setae (specimens from Myojin Knoll) or with row of 10–15 plumose setae (all longer than inner pair of lateral spines) (specimens from NW Eifuku and NW Rota seamounts).

Eyes (Figure 3A, C) incompletely fused mesially, each with small tubercle on anterodorsal surface; cornea unfaceted.

Antennular peduncle (Figure 3A, C) reaching or slightly overreaching distal margin of antennal scale. First article with strong distolateral tooth, not reaching mid-length of second article; dorsal surface with distinct, obliquely longitudinal groove; stylocerite sharp, usually reaching (rarely overreaching) mid-length of second article. Second article 1.61–1.84 times as long as wide, with small distomesial spine. Lateral flagellum sub-equal in length to carapace; mesial flagellum longer than lateral flagellum.
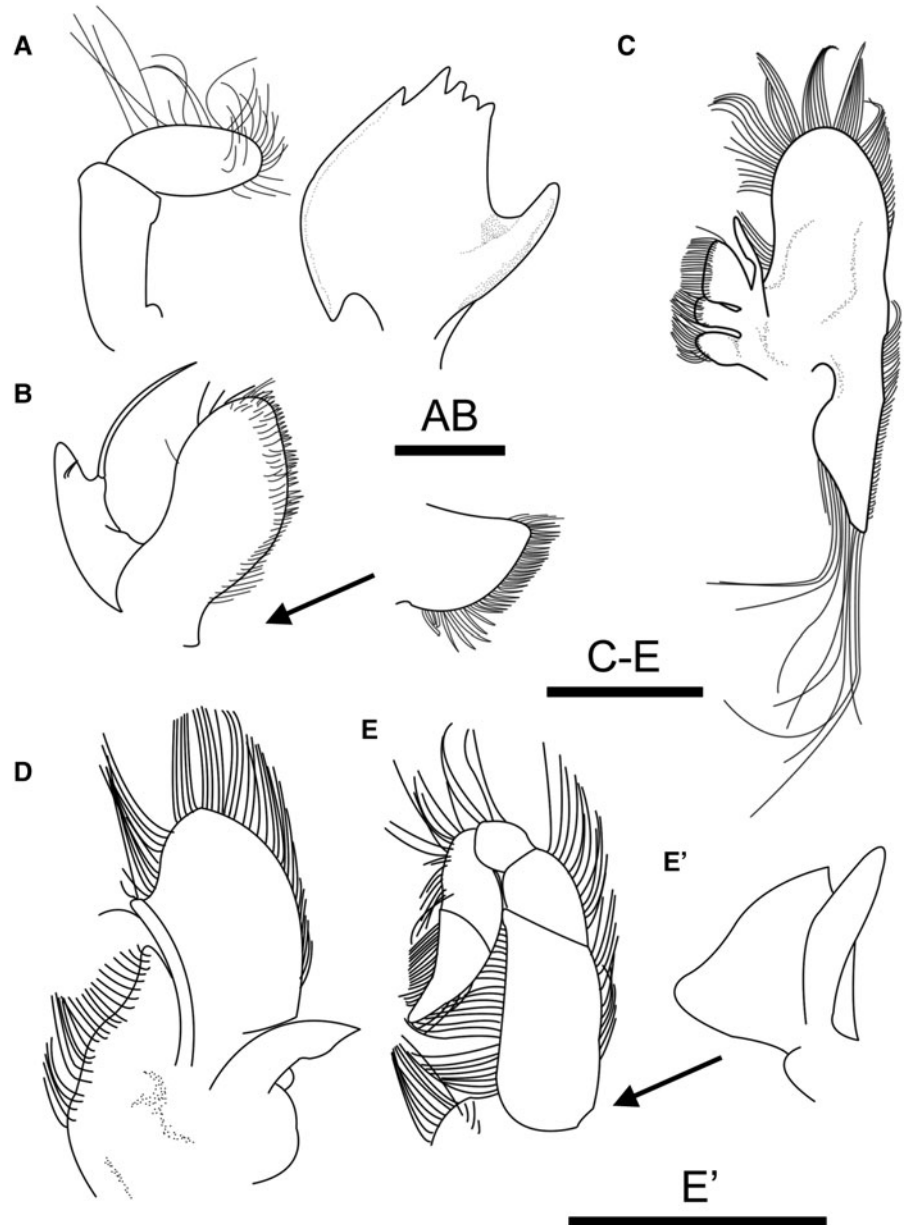
Fig. 5. *Alvinocaris marimonte* sp. nov., paratype, male (CL 10.1 mm), JAMSTEC 2050041229: (A) left mandible, inner view; (B) right maxillule, outer view; (C) left maxilla, outer view; (D) left first maxilliped, outer view; (E) left second maxilliped, outer view; (E') same, epipod and podobranch, inner view. Scale bars: A–B = 0.5 mm, C–E, E' = 1 mm.

Antenna (Figure 3A) with stout basicerite bearing moderately strong ventrolateral and weak ventral teeth. Carpocerite stout, not reaching mid-length of antennal scale. Antennal scale (Figure 3D) 1.61–2.13 times longer than wide, 0.40–0.50 length of carapace; lateral margin nearly straight; distolateral tooth directed anteriorly, falling short of broadly rounded distal margin of blade.

Mandible (Figure 5A), maxillule (Figure 5B) and maxilla (Figure 5C) typical of genus, without distinctive features. First maxilliped (Figure 5D) with exopod broad, with weak mesial projection probably representing reduced flagellum. Second maxilliped (Figure 5E) moderately stout; epipod with simple rod-like podobranch (Figure 5E). Third maxilliped (Figure 6A) usually overreaching antennal scale by 0.3–0.5 times length of ultimate article; ultimate article almost twice length of penultimate article, trigonal in cross section, subtruncate terminal margin with 3 or 4 small movable spines (Figure 6D); antepenultimate article flattened dorsoventrally, marginally setose (Figure 6B), ventrolateral distal angle with 1 slender spine; coxa stout; epipod directed laterally, slightly bi-lobed (Figure 6C).

First pereopod (Figure 6E, F) with fingers curved ventromesially; outer surface of both fingers convex, inner surface concave, cutting edges uniformly offset, closing without gap, each armed with row of closely set fine pectination; dactylus 2.0–4.0 times longer than palm, with longitudinal row of short setae on inner surface adjacent to cutting edge. Palm stout, length 0.57–0.97 of height. Carpus cupped distally to receive palm, with acute or subacute ventrodistal tooth; dorsodistal mesial margin rounded; ventromesial surface with grooming apparatus consisting of patch of dense setae and 1 minute spine. Merus and ischium unarmed, obliquely articulated.

Second pereopod (Figure 6G, H) shorter and more slender than first pereopod, not reaching distal margin of antennal scale. Fingers slightly longer than palm, each terminating in small corneous unguis crossing each other when closed; cutting edges without gap, each pectinated with a single row of small corneous teeth. Carpus subequal in length to chela. Merus and ischium obliquely articulated in lateral view. Ischium unarmed or armed with 1 spine ventrolaterally.

Third to fifth pereopods (Figure 6I–M) moderately slender, generally similar in structure and length although propodi becoming longer toward posterior, while meri becoming shorter. Dactyli (cf. Figure 6J) short (0.09–0.14 of propodal length in third, 0.10–0.12 in fourth, 0.08–0.11 in fifth), 1.92–2.55 times longer than high, each armed with 5–7 accessory spinules arranged in single
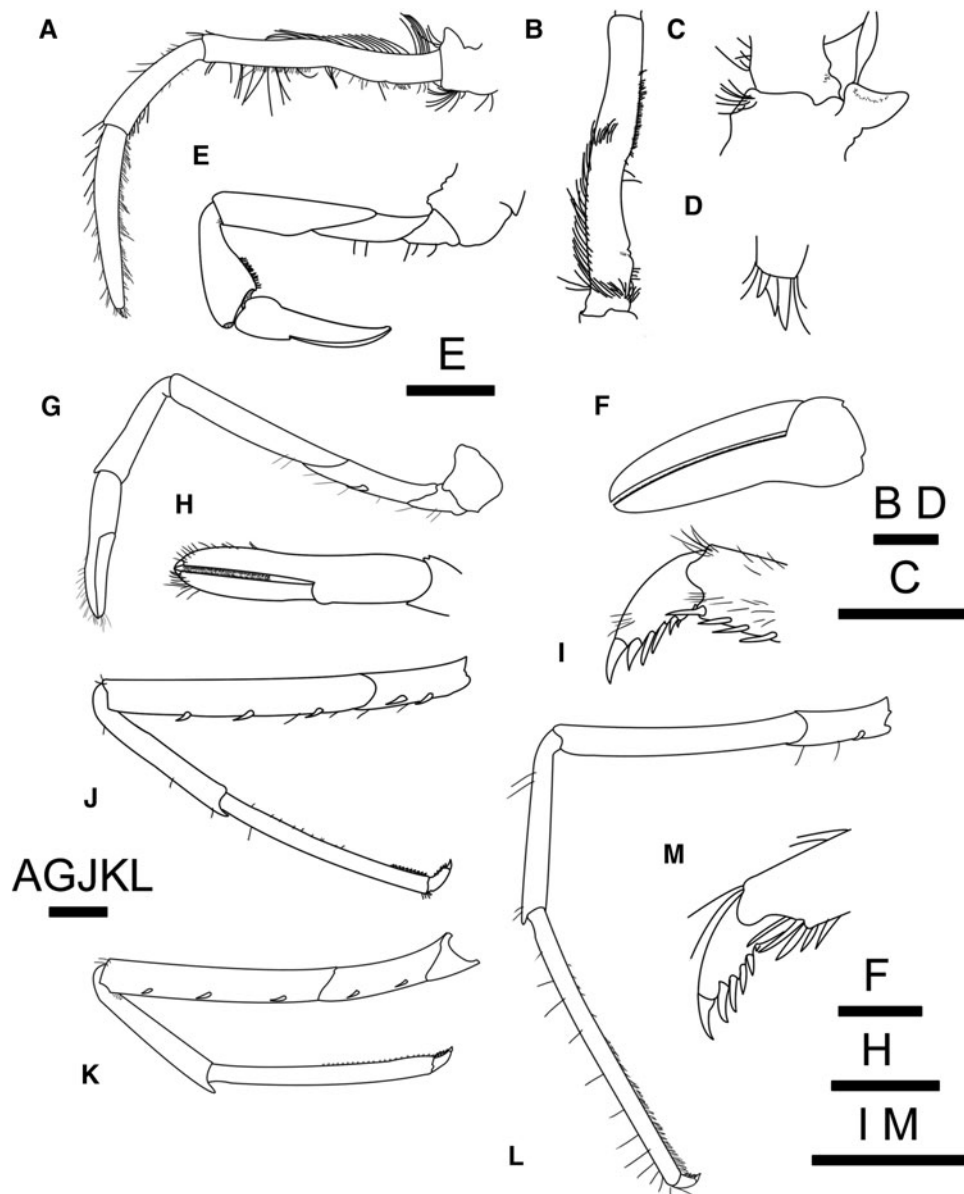
Fig. 6. *Alvinocaris marimonte* sp. nov., holotype, female (CL 9.5 mm), JAMSTEC 1130036387: (A) left third maxilliped, lateral view; (B) same, antepenultimate article, dorsomesial view; (C) same, coxa and epipod, ventral view; (D) same, distal part of ultimate article, lateral view; (E) left first pereopod, lateral view; (F) same, chela, mesial view; (G) left second pereopod, lateral view; (H) same, chela, extensor view; (I) left third pereopod, lateral view; (J) same, dactylus, lateral view; (K) left fourth pereopod, lateral view; (L) left fifth pereopod, lateral view; (M) same, dactylus and distal part of propodus. Scale bars = 1 mm.

row on flexor margin. Propodi of third and fourth pereopods with spinules arranged in 2 rows on flexor surface; propodus of fifth pereopod with numerous spinules arranged in 3 or 4 rows on distal half of ventral surface. Meri armed with 3 movable spines ventrolaterally in third, 2 or 3 spines or unarmed in fourth, unarmed in fifth. Ischia armed with 2 movable spines ventrolaterally in third, 1 or 2 spines or unarmed in fourth, and 1 spine or unarmed in fifth.

First pleopod in males with endopod (Figure 7B) about two-thirds length of exopod, distally bilobed; distomesial lobe with 2 or 3 spiniform setae directed mesially or distomesially on mesial margin; lateral margin with 8 or 9 stiff setae, and 10 or 11 setulose setae in proximal half. Appendix masculina on male second pleopod (Figure 7C) moderately robust, slightly shorter than appendix interna, with 6 or 7 spiniform setae terminally or subterminally. Uropod with exopod and endopod subequal in length, slightly overreaching telson; exopod with tiny posterolateral tooth and 1 small movable spine mesial to posterolateral tooth (Figure 4D).

Colouration in life: Body generally whitish translucent; carapace, tergites of anterior 4 pleomeres and first to fourth pleopods with tinge of pale orange (Figure 2).

Distribution: The present material was collected from Myojin Knoll (Izu-Bonin Arc, 1224 m depth), and NW Eifuku and NW Rota Seamounts (Mariana Arc; 525 m and 1574–1582 m depths, respectively). Yahagi *et al.* (2015) mentioned the occurrence of the new species (as *Alvinocaris* sp.) in the Suiyo Seamount in the Izu-Bonin Arc at a depth of 1387 m and Irabu Knoll in the Okinawa Trough at a depth of 1651 m.

Etymology: The specific epithet is the Latin 'marimonte' meaning 'seamount', referring to the occurrence of the new species in hydrothermal vents on seamounts.

Remarks: Tsuchida *et al.* (2012) recorded *Alvinocaris brevitelsonis* from the NW Eifuku Seamount at a depth of 1629 m. At present, however, only the occurrence of the present new species is confirmed from hydrothermal vents on the NW Eifuku Seamount, and thus it is likely that the previous record might actually represent *A. marimonte* sp. nov. As noted above,
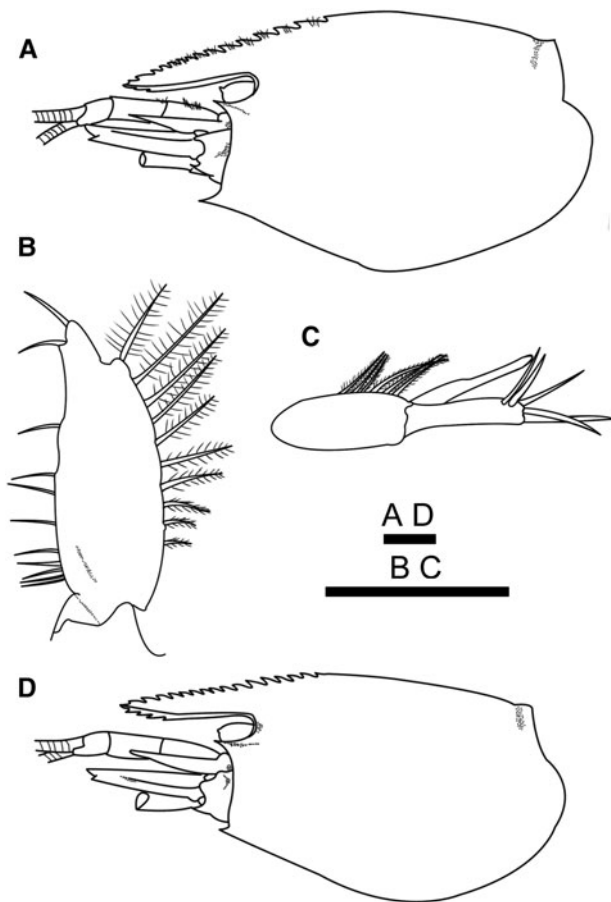
Fig. 7. *Alvinocaris marimonte* sp. nov. A, paratype, female (CL 7.0 mm), JAMSTEC 2050041227; B, C, D, paratype, male (CL 6.8 mm), JAMSTEC 2050041232 : (A, D) carapace and cephalic appendages, lateral view; (B) endopod of left first pleopod, ventral view; (C) appendices interna and masculina of left second pleopod, dorsomesial view. Scale bars = 1 mm.

A. brevitelsonis is known with certainty only from the Minami-Ensei Knoll in the Okinawa Trough (Komai & Segonzac, 2005). As mentioned above, Yahagi *et al.* (2015) mentioned the occurrence of the present new species in Suiyo Seamount, Izu-Bonin Arc and Irabu Knoll, Okinawa Trough, although we have had no opportunity to examine material from the Okinawa Trough.

Identity of the populations from Myojin Knoll, NW Eifuku and NW Rota Seamounts

Initially, it was thought that two species were represented in our collection from the Izu-Bonin and Mariana Arcs because the two morphs amongst our specimens differed in the ornamentation of the posterior margin of their telsons (spines *vs* plumose setae), a characteristic that is generally used to distinguish between species of *Alvinocaris* (cf. Kikuchi & Hashimoto, 2000; Komai & Segonzac, 2005). The first morph, represented by specimens from Myojin Knoll, has a row of spines on the posterior margin of the telson (Figure 4B), and the second morph, represented by specimens from NW Eifuku and NW Rota seamounts, has a row of plumose setae flanked by two unequal pairs of lateral spines on that margin (Figure 4C). It seemed that the variation was related to the geographic pattern. However, comparison of other morphological characters failed to detect any significant differences among the specimens of the two morphs. Furthermore, analyses based on partial sequences of the mitochondrial COI and nuclear ITS-I genes, representing molecular markers usually

useful for species discrimination (Chu *et al.*, 2001; Hebert *et al.*, 2003), showed that the two morphs could not be differentiated genetically (Tables 1 and 2): the genetic divergence between the two morphs was 0.0–1.1% (average: 0.5%) in COI (477 bp) and 0.0–0.5% (average: 0.2%) in ITS-I (552 bp), both included in ranges of the genetic divergence of specimens within respective morph. Although some examples of low genetic divergences between species in COI are known in Alvinocarididae (e.g. Vereshchaka *et al.*, 2015), considering the evidence from both morphological comparison and genetic analyses using two markers, we came to a conclusion that the two morphs represent a single species exhibiting variation in the telson posterior margin ornamentation. Nevertheless, future study using more genetic markers may eventually reveal the significance of the variation in the telson ornamentation.

Morphological comparison between Alvinocaris marimonte sp. nov. and other congeneric species

In general, species of *Alvinocaris* are morphologically very similar, and intraspecific variability often compromises the significance of supposed distinguishing characteristics (e.g. length and armature of the rostrum, development of the branchiostegal tooth of the carapace, and armature of the third to fifth pleura; cf. Komai & Segonzac, 2005). The discovery of *A. marimonte* sp. nov. has revealed that the ornamentation of the posterior margin of the telson (spines *vs* plumose setae) can vary intraspecifically in species of *Alvinocaris*. Consequently, evaluation of the differentiating characters among species of the genus should be made very carefully.

Alvinocaris marimonte sp. nov. is characterized by (i) the moderately long rostrum, which does not overreach the distal margin of the second article of the antennular peduncle and is armed with 0–4 ventral teeth, (ii) the posterior-most tooth of the dorsal rostral series located at 0.23–0.39 of CL, (iii) the slightly elevated dorsum of the carapace even in adult females (the dorsal angle 160–165°), (iv) the weakly to moderately pronounced branchiostegal tooth of the carapace, (v) pleura of the third and fourth pleomeres which sometimes bear marginal denticles, (vi) the weakly bilobed posterior margin of the telson, (vii) the moderately stout second article of the antennular peduncle (1.6–1.8 times as long as wide), and (viii) the merus and ischium of the third pereopod armed with movable spines.

Below, comparison with other species presently assigned to *Alvinocaris* is given.

(1) *Alvinocaris alexander* is distinguished from *A. marimonte* sp. nov. by (i) the more strongly elevated dorsum of the carapace in females (the dorsal angle is ∼145° in *A. alexander*), (ii) the more pronounced branchiostegal tooth, (iii) the convex posterior margin of the telson and (iv) the stouter second article of the antennular peduncle (length 1.25–1.31 times width) (cf. Ahyong, 2009). *Alvinocaris alexander* is presently known only from the Brothers Caldera and Rumble V Seamount, Kermadec Ridge (south-western Pacific), at depths of 367–1346 m.

(2) *Alvinocaris brevitelsonis* is so far represented only by the holotype, and thus evaluation of intraspecific variation of the species is not possible. Nevertheless, *A. brevitelsonis* differs from the new species by (i) the relatively longer rostrum (reaching the distal margin of the second article of the antennular peduncle), (ii) more numerous ventral teeth of the rostrum (seven teeth are present), (iii) the more strongly elevated dorsum of the carapace in the adult female (dorsal angle of 150°) and (iv) the evenly convex posterior margin of the telson (Kikuchi & Hashimoto, 2000; Komai & Segonzac,

Table 1. K2P genetic divergence of the partial sequences of the mitochondrial COI gene among the nine individuals of *A. marimonte* sp. nov. Two sequences registered under the name *Alvinocaris* sp. (LCO029852, Suiyo Sea mount; and LCO029859, Irabu Knoll, Okinawa Trough) (Yahagi *et al.*, 2015) are also included in the analysis

Species	1	2	3	4	5	6	7	8	9
1. MK									
2. MK	0.004								
3. NWE	0.006	0.002							
4. NWE	0.008	0.008	0.011						
5. NWE	0.004	0.004	0.006	0.004					
6. NWE	0.006	0.006	0.008	0.002	0.002				
7. NWR	0.006	0.006	0.008	0.002	0.002	0.000			
8. *Alvinocaris* sp. LC029852 (Suiyo)	0.004	0.000	0.002	0.008	0.004	0.006	0.006		
9. *Alvinocaris* sp. LC029859 (Irabu)	0.004	0.004	0.006	0.004	0.000	0.002	0.002	0.004	

MK, Myojin Knoll; NEW, North-west Eifuku Seamount; NWR, North-west Rota Seamount.

Table 2. K2P genetic divergence of the partial sequence of the nuclear DNA ITS-I gene among the seven individuals of *A. marimonte* sp. nov.

Specimens	1	2	3	4	5	6	7
1. MK							
2. MK	0.004						
3. NEW	0.004	0.000					
4. NEW	0.004	0.000	0.000				
5. NEW	0.004	0.000	0.000	0.000			
6. NEW	0.004	0.000	0.000	0.000	0.000		
7. NWR	0.005	0.002	0.002	0.002	0.002	0.002	

MK, Myojin Knoll; NEW, North-west Eifuku Seamount; NWR, North-west Rota Seamount.

2005). *Alvinocaris brevitelsonis* is known only from the Minami-Ensei Knoll, Okinawa Trough (north-western Pacific), at a depth of 705 m (Kikuchi & Hashimoto, 2000; Komai & Segonzac, 2005).

(3) *Alvinocaris chelys* is distinguished from *A. marimonte* sp. nov. by (i) the ventral margin of the rostrum, which is unarmed or armed with one minute subterminal tooth, (ii) the more strongly elevated dorsum of the carapace in adult females (dorsal angle ~155° in *A. chelys*), (iii) the third and fourth pleonal pleura which are always unarmed in *A. chelys*, (iv) the stouter second article of the antennal peduncle (1.3–1.4 times as long as wide in *A. chelys* vs 1.6–1.8 times in *A. marimonte* sp. nov.), (v) fewer meral spines on the third pereopod (unarmed or only with one spine) and (vi) the unarmed ischium of the third pereopod (cf. Komai & Chan, 2010). *Alvinocaris chelys* is known only from Gueishandao, off north-eastern Taiwan (north-western Pacific), at depths of 252–300 m (Komai & Chan, 2010).

(4) *Alvinocaris costaricensis* is distinguished from *A. marimonte* sp. nov. by (i) the relatively longer rostrum (usually over-reaching the distal margin of the antennular peduncle), (ii) the more numerous rostral ventral teeth (5–7) and (iii) the possession of only two movable spines on the merus of the third pereopod (vs three spines in *A. marimonte* sp. nov.). *Alvinocaris costaricensis* was recently described from a methane seep off Costa Rica, eastern Pacific, at depths of 1001–1800 m (Martin *et al.*, 2018).

(5) *Alvinocaris dissimilis* can be differentiated from *A. marimonte* sp. nov. by (i) the more strongly elevated dorsum of the carapace (dorsal angle ~155°), (ii) the convex posterior margin of the telson and (iii) the always unarmed third pleuron (cf. Komai & Segonzac, 2005). *Alvinocaris dissimilis* is known from the Minami-Ensei Knoll, Okinawa Trough, at depths of 691–705 m (Komai & Segonzac, 2005; Yahagi *et al.*, 2015).

(6) *Alvinocaris kexueae* differs from *A. marimonte* sp. nov. in (i) the relatively longer rostrum (usually overreaching the margin end of the antennular peduncle), (ii) the more numerous rostral ventral teeth (five or six), (iii) the more posteriorly located posterior-most tooth of the dorsal rostral series (located at the 0.4 of CL) and (iv) the presence of a small median tooth on the posterior margin of the telson (vs no median tooth in *A. marimonte* sp. nov.) (cf. Wang & Sha, 2017). *Alvinocaris kexueae* is known from hydrothermal vents on the Manus Basin, Bismarck Sea, south-western Pacific, at depths of 1714–1910 m.

(7) *Alvinocaris longirostris* is easily distinguished from *A. marimonte* sp. nov. by (i) the relatively longer rostrum (usually overreaching the distal margin of the antennular peduncle), (ii) the more numerous rostral ventral teeth (four to nine), (iii) the more posteriorly arising posterior-most tooth of the dorsal rostral series (arising at 0.38–0.48 of CL), (iv) the more elevated dorsum of the carapace (dorsal angle ~150°), (v) the more strongly pronounced branchiostegal tooth on the carapace and (vi) the convex posterior margin of the telson (Kikuchi & Ohta, 1995; Komai & Segonzac, 2005). *Alvinocaris longirostris* is known with certainty from the north-west Pacific localities, i.e. hydrothermal vents on the Iheya Ridge, Irabu Knoll and Hatoma Knoll, Okinawa Trough, and cold seeps in Sagami Bay (off

Table 3. K2P genetic divergence of the partial sequences of the mitochondrial COI gene among the 12 species of *Alvinocaris*

Species	1	2	3	4	5	6
1. *Alvinocaris marimonte* sp. nov.						
2. *Alvinocaris muricola*	0.160					
3. *Alvinocaris markensis*	0.157	0.004				
4. *Alvinocaris longirostris*	0.163	0.057	0.052			
5. *Alvinocaris lusca*	0.169	0.063	0.058	0.047		
6. *Alvinocaris chelys*	0.164	0.166	0.166	0.193	0.198	
7. *Alvinocaris dissimilis*	0.168	0.166	0.166	0.193	0.198	0.006
8. *Alvinocaris stactophila*	0.165	0.165	0.165	0.192	0.197	0.003
9. *Alvinocaris komaii*	0.164	0.182	0.182	0.196	0.201	0.199
10. *Alvinocaris solitaire*	0.171	0.107	0.104	0.135	0.142	0.166
11. *Alvinocaris kexueae*	0.168	0.103	0.101	0.131	0.131	0.157
12. *Alvinocaris costaricensis*	0.117	0.192	0.192	0.196	0.214	0.167
Species	**7**	**8**	**9**	**10**	**11**	**12**
1. *Alvinocaris marimonte* sp. nov.						
2. *Alvinocaris muricola*						
3. *Alvinocaris markensis*						
4. *Alvinocaris longirostris*						
5. *Alvinocaris lusca*						
6. *Alvinocaris chelys*						
7. *Alvinocaris dissimilis*						
8. *Alvinocaris stactophila*	0.003					
9. *Alvinocaris komaii*	0.200	0.200				
10. *Alvinocaris solitaire*	0.166	0.165	0.154			
11. *Alvinocaris kexueae*	0.163	0.161	0.162	0.063		
12. *Alvinocaris costaricensis*	0.172	0.169	0.142	0.174	0.155	

Hatsushima Site) and in the South China Sea (Jiaolong Cold Seep I), at depths of 1053–1627 m (Yahagi *et al.*, 2015; Li, 2015). Webber (2004) identified specimens from the Brothers Caldera, Kermadec Ridge, New Zealand, at depths of 1200–1850 m, with *A. longirostris*, but this identification needs to be verified.

(8) *Alvinocaris markensis* and *A. muricola* differ from *A. marimonte* sp. nov. in (i) the relatively long rostrum (usually reaching or overreaching the distal margin of the second article of the antennular peduncle), (ii) the more numerous ventral teeth on the rostrum (six to nine), (iii) the more strongly elevated dorsum of the carapace (dorsal angle ∼150°), (iv) the more strongly pronounced branchiostegal tooth on the carapace and (v) the convex posterior margin of the telson (cf. Komai & Segonzac, 2005). *Alvinocaris markensis* has been reported from hydrothermal vents on the Mid-Atlantic Ridge, at depths of 1693–3650 m, and *A. muricola* has been reported from cold seeps on both sides of the Atlantic (viz., Gulf of Mexico, Barbados Accretionary Prism, Blake Ridge Diapir, and the West African equatorial margin in the Congo Basin), at depths of 1697–3277 m (Komai & Segonzac, 2005). Teixeira *et al.* (2013) has shown that the two taxa are genetically identical based on partial sequences of the mitochondrial COI gene, suggesting that *A. markensis* and *A. muricola* are conspecific.

(9) *Alvinocaris methanophila* has (i) more numerous rostral ventral teeth (3–11), (ii) a more strongly elevated dorsum

of the carapace (dorsal angle ∼155° *vs* 160–165°), (iii) a more strongly pronounced branchiostegal tooth on the carapace and (iv) the convex posterior margin of the telson (Komai *et al.*, 2005). It is known only from the Blake Ridge Diapir, off North Carolina, north-western Atlantic, at depths of 2155–2167 m.

(10) *Alvinocaris solitaire* is easily distinguished from *A. marimonte* sp. nov. by (i) the relatively longer rostrum (overreaching the distal margin of the second article of antennular peduncle), (ii) the more posteriorly arising posterior-most tooth of the dorsal rostral series (located at the 0.45 of CL) and (iii) the more slender second article of the antennular peduncle (1.95 times as long as wide *vs* 1.6–1.8 times as long) (Yahagi *et al.*, 2014). *Alvinocaris solitaire* is known only from Solitaire hydrothermal vent fields, Central Indian Ridge, Indian Ocean, at a depth of 2606 m.

(11) *Alvinocaris stactophila* appears unique within the genus in the armature of the posterior margin of the telson (the mesial pair of the two posterolateral pairs of spines of the telson is noticeably incurved), and the flexor margin of the dactylus of the third pereopod (which bears penultimate and antepenultimate spinules that are distinctly longer than the ultimate and proximal spinules) (Komai & Segonzac, 2005). In other species of *Alvinocaris*, including the present new species, the mesial pair of posterolateral spines is almost straight, and the accessory spinules on the
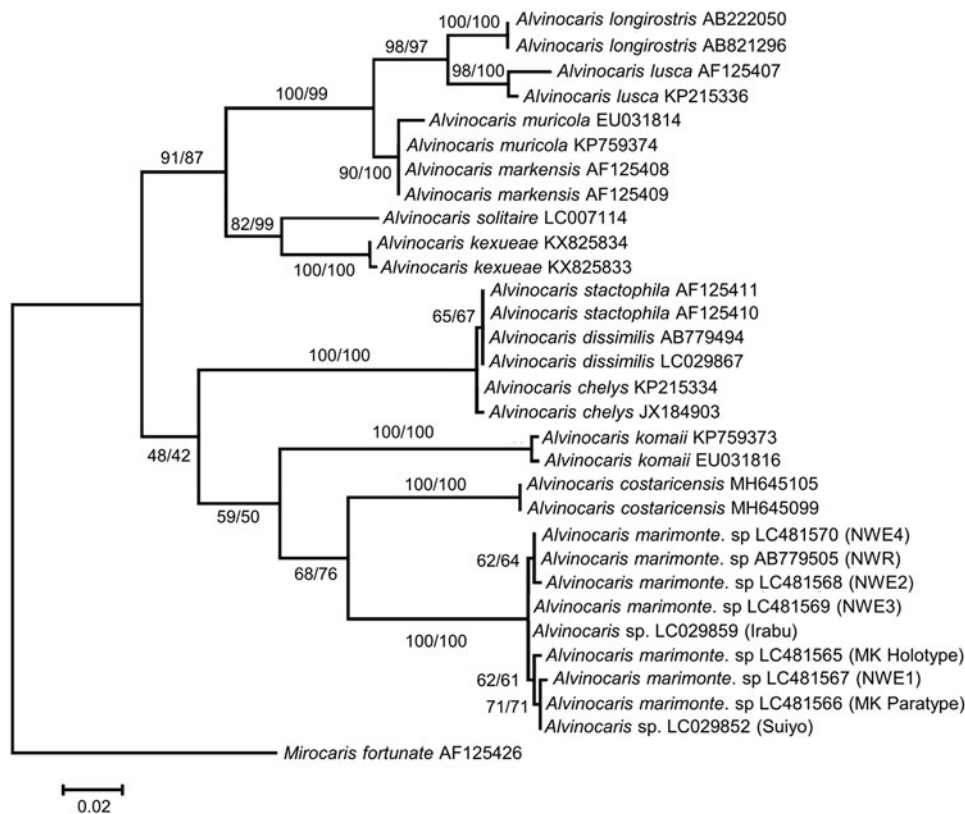
Fig. 8. The Maximum-likelihood (ML) tree of *Alvinocaris* and outgroup inferred from partial COI sequences (477 bp) using K2P distances. *Mirocaris fortunata* (AF125426) used as an outgroup. Bootstrap values in ML are given for branches with NJ values (ML/NJ) obtained by 1000 replicate sampling, respectively. MK, Myojin Knoll; NWE, North-west Eifuku Seamount; NWR, North-west Rota Seamount.

dactylus of the third pereopod become gradually shorter, proximally. Furthermore, the convex posterior margin of the telson distinguishes *A. stactophila* from *A. marimonte* sp. nov. *Alvinocaris stactophila* is known from cold seeps on the Louisiana Slope, northern Gulf of Mexico, at depths of 534–650 m (Williams, 1988; Komai & Segonzac, 2005).

(12) *Alvinocaris williamsi* differs from *A. marimonte* sp. nov. in (i) the more robustly built body, (ii) the ventrally unarmed rostrum, (iii) the proportionally wider telson with dorsolateral spines arranged in a slightly curved row, (iv) the relatively stout antennal peduncle (the length–width ratio 1.3–1.4 in *A. williamsi*), (v) the relatively wider antennal scale (1.4–1.5 times as long as wide in *A. williamsi* vs 1.6–2.1 times as long in *A. marimonte* sp. nov.) and (vi) the unarmed ischia of the third and fourth pereopods (Shank & Martin, 2003; Komai & Segonzac, 2005). *Alvinocaris williamsi* is known only from hydrothermal vents on Menez Gwen, Mid-Atlantic Ridge, at depths of 850–865 m.

(13) *Alvinocaris komaii* and *A. niwa* are readily distinguished from all other species of *Alvinocaris*, including *A. marimonte* sp. nov., by having (i) two or more rows of accessory spinules on the flexor margins of the dactyli of the last three pairs of pereopods (Webber, 2004; Zelnio & Hourdez, 2009). Future study may reveal sufficient differences between these two species and all other congeners to assign them to a different genus altogether. Furthermore, *A. niwa* differs from *A. marimonte* sp. nov. in having (ii) a short rostrum that does not reach the distal margin of the first article of the antennular peduncle and (iii) unarmed meri of the third and fourth pereopods (Webber, 2004). *Alvinocaris komaii* has (ii) very characteristic strong postrostral teeth on the carapace and (iii) a deeply bilobed posterior margin of the telson (Zelnio & Hourdez, 2009; Komai & Tsuchida, 2015). *Alvinocaris komaii* occurs in the south-western Pacific hydrothermal vents (Lau Basin, Manus Basin,

Vanuatu and Futuna Islands, at depths of 1406–2750 m) (Zelnio & Hourdez, 2009; Komai & Tsuchida, 2015; Komai *et al.*, 2016); *A. niwa* is restricted to the Brothers Caldera and Rumble V Seamount, Kermadec Ridge, at depths of 367–1346 m.

(14) *Alvinocaris lusca* appears morphologically most similar to the new species. However, *A. lusca* differs from *A. marimonte* sp. nov. in that (i) it has relatively larger postrostral teeth on the carapace (cf. Komai & Segonzac, 2005: figures 5A, C and figures 4A, 8A, D) and (ii) a relatively wider antennal scale (cf. Komai & Segonzac, 2005: figure 5D and figure 4D). Furthermore, whereas in *A. marimonte* sp. nov., the third pleonal pleuron can have marginal denticles (although sometimes absent), in *A. lusca*, it is always unarmed. *Alvinocaris lusca* known from the East Pacific Rise 9°N, at depths of 2450–2520 m (Williams & Chace, 1982; Komai & Segonzac, 2005).

Genetic analyses of Alvinocaris

In this study, partial sequences of the mitochondrial COI gene (477 bp) of the 12 species of *Alvinocaris* were available for comparison, viz., *A. chelys*, *A. costaricensis*, *A. dissimilis*, *A. kexueae*, *A. komaii*, *A. longirostris*, *A. lusca*, *A. markensis*, *A. muricola*, *A. solitaire* and *A. stactophila* (Shank *et al.*, 1999; Zelnio & Hourdez, 2009; Yahagi *et al.*, 2014; Wang & Sha, 2017; Martin *et al.*, 2018). In the ML and NJ trees are almost congruent, and two major clades are evident (Figure 8). *Alvinocaris marimonte* sp. nov. is clustered with *A. costaricensis*, although the bootstrap values are rather low (68 and 76% in ML and NJ), and thus the relationship is not well supported. Indeed, morphology does not support such a close relationship between the two species (see above). Consequently, the sister relationship of *A. marimonte* with *A. costaricensis* might not actually be correct. The K2P genetic divergences between the new species and the other congeneric species range between 11.7–17.1%, well

supporting the recognition of the present new species. The genetic divergence between the new species and the closest species, *A. constaricensis*, is 11.7%. The morphologically most similar species to the new species is *A. lusca*, but the genetic divergence between the two is 16.9%, suggesting that they might not be sister species (Table 3).

References

Ahyong ST (2009) New species and new records of hydrothermal vent shrimps from New Zealand (Caridea: Alvinocarididae, Hippolytidae). *Crustaceana* **82**, 775–794.

Chu KH, Li CP and Ho HY (2001) The first internal transcribed spacer (ITS-1) of ribosomal DNA as a molecular marker for phylogenetic and population analyses in Crustacea. *Marine Biotechnology* **3**, 355–361.

Folmer O, Black M, Hoeh W, Lutz R and Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Hebert PD, Cywinska A, Ball SL and de Waard JR (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B* **270**, 313–321.

Kikuchi T and Ohta S (1995) Two caridean shrimps of the families Bresiliidae and Hippolytidae from a hydrothermal field on the Iheya Ridge, off the Ryukyu Islands, Japan. *Journal of Crustacean Biology* **15**, 771–785.

Kikuchi T and Hashimoto J (2000) Two new caridean shrimps of the family Alvinocarididae (Crustacea, Decapoda) from a hydrothermal field at the Minami-Ensei knoll in the Mid-Okinawa Trough, Japan. *Species Diversity* **5**, 135–148.

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**, 111–120.

Komai T and Segonzac M (2004) A new genus and species of alvinocaridid shrimp (Crustacea: Decapoda: Caridea) from hydrothermal vents on the North Fiji and Lau Basins, south-western Pacific. *Journal of the Marine Biological Association of the United Kingdom* **84**, 1179–1188.

Komai T and Segonzac M (2005) A revision of the genus Alvinocaris Williams and Chace (Crustacea: Decapoda: Caridea: Alvinocarididae), with descriptions of a new genus and a new species of Alvinocaris. *Journal of Natural History* **39**, 1111–1175.

Komai T and Chan TY (2010) A new genus and two new species of alvinocaridid shrimps (Crustacea: Decapoda: Caridea) from a hydrothermal vent field off northeastern Taiwan. *Zootaxa* **2372**, 15–32.

Komai T and Tsuchida S (2015) New records of Alvinocarididae (Crustacea: Decapoda: Caridea) from the southwestern Pacific hydrothermal vents, with descriptions of one new genus and three new species. *Journal of Natural History* **49**, 1789–1824.

Komai T and Giguère T (2019) A new species of the alvinocaridid shrimp genus Rimicaris Williams & Rona, 1986 (Decapoda: Caridea) from hydrothermal vents on the Mariana Back Arc Spreading Center, northwestern Pacific. *Journal of Crustacean Biology*. doi: 10.1093/jcbiol/ruz046.

Komai T, Shank TM and Van Dover CL (2005) A new species of Alvinocaris (Crustacea: Decapoda: Caridea: Alvinocarididae) and a new record of A. muricola from methane seeps on the Blake Ridge Diapir, Northwestern Atlantic. *Zootaxa* **1019**, 27–42.

Komai T, Menot L and Segonzac M (2016) New records of caridean shrimp (Crustacea: Decapoda) from hydrothermally influenced fields off Futuna Island, Southwest Pacific, with description of a new species assigned to the genus Alvinocaridinides Komai & Chan, 2010 (Alvinocarididae). *Zootaxa* **4098**, 298–310.

Kumar S, Stecher G and Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**, 1870–1874.

Li X (2015) Report on two deep-water caridean shrimp species (Crustacea: Decapoda: Caridea: Alvinocarididae, Acanthephyridae) from the northeastern South China Sea. *Zootaxa* **3911**, 130–138.

Martin JW and Christiansen JC (1995) A new species of the shrimp genus Chorocaris Martin and Hessler, 1990 (Crustacea, Decapoda, Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge. *Proceedings of the Biological Society of Washington* **108**, 220–227.

Martin JW, Wall AR, Shank T, Cha H, Seid CA and Rouse GW (2018) A new species of Alvinocaris (Crustacea: Decapoda: Caridea: Alvinocarididae) from Costa Rican methane seeps. *Zootaxa* **4504**, 418–430.

Shank TM and Martin JW (2003) A new caridean shrimp of the family Alvinocarididae from thermal vents at Menez Gwen on the Mid-Atlantic Ridge. *Proceedings of the Biological Society of Washington* **116**, 158–167.

Shank TM, Black MB, Halanych KM, Lutz RA and Vrijenhoek RC (1999) Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochondrial cytochrome oxidase subunit I. *Molecular Phylogenetics and Evolution* **13**, 244–254.

Teixeira S, Karine O, Decker C, Cunha RL, Fuchs S, Hourdez S, Serrão EA and Arnaud-Haond S (2013) High connectivity across the fragmented chemosynthetic ecosystems of the deep Atlantic Equatorial Belt: efficient dispersal mechanisms or questionable endemism? *Molecular Ecology* **22**, 4663–4680.

Tsuchida S, Yamaguchi T, Komai T and Watanabe H (2012) *Alvinocaris brevitelsonis* Kikuchi & Hashimoto, 2000. In Fujikura K, Okutani T and Maruyama T (eds), *Deep-Sea Life – Biological Observations Using Research Submersibles*, 2nd Edn. Hatano: Tokai University Press, p. 188.

Vereshchaka AL (1997) A new family for a deep-sea caridean shrimp from North Atlantic hydrothermal vents. *Journal of the Marine Biological Association of the United Kingdom* **77**, 425–438.

Vereshchaka AL, Kulagin DN and Lunina AA (2015) Phylogeny and new classification of hydrothermal vent and seep shrimps of the family Alvinocarididae (Decapoda). *PLoS ONE* **10**, e0129975.

Wang YR and Sha ZL (2016) A new species of the genus Manuscaris Komai & Tsuchida, 2015 (Decapoda, Caridea, Alvinocarididae) from the Manus Basin hydrothermal vents. *Crustaceana* **89**, 1541–1550.

Wang YR and Sha ZL (2017) A new species of the genus Alvinocaris Williams and Chace, 1982 (Crustacea: Decapoda: Caridea: Alvinocarididae) from the Manus Basin hydrothermal vents, Southwest Pacific. *Zootaxa* **422**, 126–136.

Webber WR (2004) A new species of Alvinocaris (Crustacea: Decapoda: Alvinocarididae) and new records of alvinocaridids from hydrothermal vents north of New Zealand. *Zootaxa* **444**, 1–26.

Williams AB (1988) New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage. *Fishery Bulletin* **8**, 263–287.

Williams AB and Chace Jr FA (1982) A new caridean shrimp of the family Bresiliidae from thermal vents of the Galapagos Rift. *Journal of Crustacean Biology* **2**, 136–147.

Williams AB and Rona PA (1986) Two new caridean shrimps (Bresiliidae) from a hydrothermal field on the Mid-Atlantic Ridge. *Journal of Crustacean Biology* **6**, 446–462.

Williams AB and Dobbs FC (1995) A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii. *Proceedings of the Biological Society of Washington* **108**, 228–237.

Yahagi T, Watanabe H, Kojima S, Beedessee G and Komai T (2014) First record and a new species of Alvinocaris Williams & Chace, 1982 (Crustacea: Decapoda: Caridea: Alvinocarididae) from the Indian Ocean. *Zootaxa* **3893**, 101–113.

Yahagi T, Watanabe H, Ishibashi J and 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.

Zelnio KA and Hourdez S (2009) A new species of Alvinocaris (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vents at the Lau Basin, southwest Pacific, and a key to the species of Alvinocarididae. *Proceedings of the Biological Society of Washington* **122**, 52–71.