

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

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Abstract.—We describe *Alvinocaris komaii*, new species, from hydrothermal fields at the Eastern Lau Spreading Center (ELSC). Adults of this species are distinguished in the field from other alvinocaridids at the ELSC by their larger size and orange-white carapace. Additionally, they appear to preferentially inhabit mussel beds composed of *Bathymodiolus brevior*. *Alvinocaris komaii* differs from all known species in the genus by a distinctive deep notch mesially on the telson and accessory spinules on the dactyli of the third to fifth pereopods arranged in 2 rows. A suite of morphological characters separates *A. komaii* from other alvinocaridids. We analyze the degree of morphological variation in *A. komaii* and discuss affinities of the Pacific species of *Alvinocaris*. Molecular data from the mitochondrial COI gene is used to compliment this description, and a key to the species of the family Alvinocarididae is included with locality information.

Caridean shrimp of the family Alvinocarididae Christoffersen, 1986 (see also Komai & Segonzac 2003) are well documented from hydrothermal vents and cold seeps worldwide (Komai & Segonzac 2005, Martin & Haney 2005). This family is composed of 7 genera: *Alvinocaris* Williams & Chace, 1982, *Rimicaris* Williams & Rona, 1986, *Chorocaris* Martin & Hessler, 1990, *Opaepele* Williams & Dobbs, 1995, *Mirocaris* Vereshchaka, 1997, *Nautilocaris* Komai & Segonzac, 2004, and *Shinkaicaris* Komai & Segonzac, 2005. *Alvinocaris* is the most species-rich genus in the Alvinocarididae, with 10 previously described species represented by six vent-endemic species and four seep-

endemic species from nearly all known sites in the Atlantic and Pacific Oceans. Species in the genus *Alvinocaris* have not been reported from non-chemosynthetic environments. Escobar-Briones & Villalobos-Hiriart (2003) noted an “*Alvinocaris* sp.” off the Banco Chinchorro in 176–203 m water depth but provided no taxonomic or descriptive details.

At the Eastern Lau Spreading Center (ELSC, Fig. 1), a Ridge2000 designated Integrated Studies Site, two alvinocaridid shrimp, *Chorocaris vandoverae* Martin & Hessler, 1990 and *Nautilocaris saintlaurientae* Komai & Segonzac, 2004, and one hippolytid shrimp, *Lebbeus* sp., have been identified from collections and video during recent expeditions to the ELSC. We describe a new species of *Alvinocaris* from hydrothermal vents at the ELSC. This

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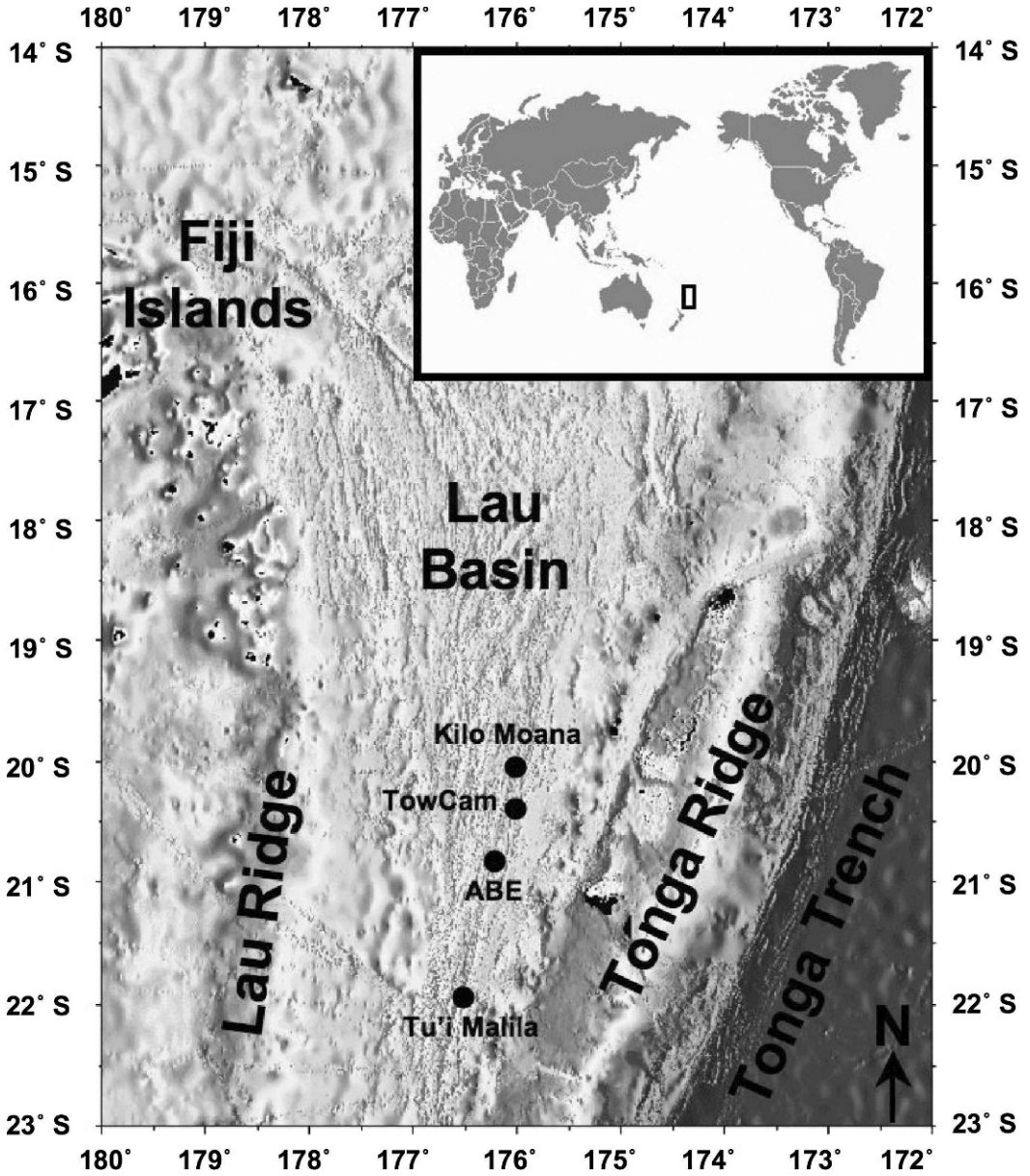


Fig. 1. Map of collection sites at the Lau Basin with topographic features. Background image is courtesy of the Ridge Multibeam Synthesis Data Portal of the Marine Geoscience Data System.

species represents the fourth genus of caridean shrimp reported from the ELSC and eleventh species in the genus *Alvinocaris*.

Materials and Methods

Specimens were collected during the June 2005 TUIM07MV and September

2006 MGLN07MV cruises to the ELSC. Collection was done using the JASON II remotely operated vehicle and brought onboard the R/V *Melville* for study. Tools used to collect individuals were the manipulator arm, suction sampler, and the mussel pot, a quantitative collection device to collect intact samples of mussel

and snail bed communities. Specimens studied came from the following sites (Fig. 1): Kilo Moana (20°9'S, 176°12'E, 2620 m) dives J2-154 (1 female), J2-164 (9 females, 1 male, 1 indeterminate), J2-230 (1 female) and J2-235 (19 females, 6 males, 2 indeterminate), TowCam (20°19'S, 176°8'E, 2700 m) during dive J2-240 (3 indeterminate), and ABE (20°45'S, 176°11'E, 2145 m) during dive J2-237 (7 females, 2 males). Indeterminate individuals were missing their pleopodal half; therefore, they could not be sexed by examining the appendix masculina. We confirmed by video that the new species described herein is also present at Tu'i Malila (21°59'S, 176°34'E, 1880 m, Fig. 1). No juveniles were obtained in our collections. Females collected in either June 2005 or September 2006 were not carrying eggs.

Holotype and paratype specimens are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. [holotype USNM (1116499), paratypes USNM (1116500–04)]. Additional voucher material is held in the laboratory of Dr. Charles R. Fisher in the Department of Biology at Pennsylvania State University (University Park, Pennsylvania, U.S.A.).

The descriptive terminology used follows that of Komai & Segonzac (2005). Carapace length was measured from the posterior margin of the orbit level to the posterior margin of the carapace. Rostral length was measured from the anterior-most part of the rostrum to the posterior margin of the orbit. Carapace width was measured from the widest sections of the branchial regions. The total length was measured from the anterior-most part of the rostrum to the posterior margin of the telson. Stata (Intercooled Stata version 9.2, College Station, Texas U.S.A.) was used to analyze morphometric data. One-way ANOVA was used to test differences in characters between sites and gender, using Bonferroni correction for multiple

comparisons when appropriate. Linear regression was used to test the significance of the relationship between continuous characters.

Frozen tissues (ca. 0.2 g) were digested overnight with proteinase K at 55°C in 0.5 ml PK-SDS lysis buffer (Tris-HCl 50 mM pH 8.0, NaCl 100 mM, 10 mM EDTA, 1% SDS). Genomic DNA was purified using standard phenol/chloroform extractions and stored at 4°C in TE (Tris 10 mM, 1 mM EDTA pH 8.0). The mitochondrial gene coding for cytochrome oxidase subunit I (COI) was amplified with the primers used by Folmer et al. (1994) and following the conditions reported in Black et al. (1997).

Sequences of each strand were generated by using chain-terminating fluorescently labeled nucleotides with universal primer T3 or T7 and the Big Dye® Terminator V3.1 Cycle Sequencing kit (Applied Biosystems). Reactions were subsequently run on a 16-capillary 3130 Applied Biosystems sequencer. The 2 COI sequence strands for each species were assembled and proofread in CodonCode Aligner to generate a continuous fragment. Sequences were aligned manually.

In addition to the species already available in the GenBank database (see Fig. 7 for accession numbers), sequences for 2 species were used for this study: the new species described herein (two individuals from ABE were used and yielded an identical sequence) and *Alvinocaris muricola* Williams, 1988 from the Florida Escarpment in the Gulf of Mexico [one individual, 3200 m, for more details on collection site, see Cordes et al. (2007)], and from the REGAB area of the Gulf of Guinea [one individual, 3160 m, for more details on the site, see Ondréas et al. (2005)]. The sequence from *Lebbeus carinatus* de Saint Laurent, 1984 (Hippolytidae) was used as an outgroup. The tree was constructed using the Neighbor Joining method on Kimura-2-Parameter distances on a 600-bp alignment. Boot-

strap values were calculated on 1000 resampling replicates.

Alvinocaris komaii, new species

Figs. 1–6

Material examined.—Holotype: female, Kilo Moana, TL = 61.4 mm, CL = 15.4 mm, CW = 8.8 mm, RL = 5.6 mm. Paratypes: males ($n = 9$)—TL = 60.0–72.7 mm, CL = 13.3–16.9 mm, CW = 7.9–11.2 mm, RL = 7.1–9.5 mm; females ($n = 36$)—TL = 43.9–92.2 mm, CL = 9.8–23.2 mm, CW = 5.7–14.2 mm, RL = 5.1–14.9 mm; indeterminate ($n = 7$)—TL = posterior ends broken, CL = 14.0–18.3 mm, CW = 7.8–11.3 mm, RL = 6.1–9.4 mm.

Carapace (Fig. 2a, b).—Integument thin, reflective, minutely punctuate. Rostrum almost distally curved, perceptibly elevated above horizontal in distal half, sharply pointed tip, reaching one-third to three-quarters length of second peduncular article of antennule; one-quarter to one-third the carapace length; dorsal margin raised into thin serrate crest containing 9–12 teeth (4–6 teeth on carapace proper) of decreasing strength toward distal end, about two-thirds length of crest is continued onto carapace, posterior-most tooth arising from two-thirds carapace length, base of rostrum deflecting from dorsal line of carapace at approximately 15°. Ventral margin less prominent and armed with 2–6 subterminal teeth. Sample rostral tooth formulas (dorsal/ventral) from the 2005 specimens are 12/6, 10/2, 10/4, 10/4, 10/2, 10/3, 9/4, 10/4, 11/4, and 9/6. Lateral carina broadened proximally and confluent with orbital margin. Carapace with acuminate antennal spine distinct, pterygostomial spine acuminate and prominent. Prominent antennal carina curving posteroventrally to intersect obliquely with carina extending from pterygostomial spine at about mid-length of carapace, associated groove continuing indistinctly posterior.

Abdomen (Fig. 2a).—Abdomen of both male and female broadly arched dorsally,

narrowest part of sixth somite about one-half the width of first somite; fourth somite drawn posterolaterally to acuminate spine, flanked dorsally by 0–4 much more slender and smaller spines; posterolateral corner of fifth pleuron acuminate and dorsally with 2–4 spines analogous to those on fourth somite; sixth somite with mid-dorsal length about 1.5–1.8 that of fifth and 1.2–1.8 as long as wide, smaller posterolateral spine acute; only fifth somite with strong, posteriorly directed spine on sternite.

Telson (Fig. 2d, e).—Telson elongate, subrectangular; length about 2.4–2.9 anterior width, 2.9–3.3 posterior width, and about 1.4–1.8 length of sixth somite, not including posterior spines; armed with 7 pairs of dorsolateral spines of nearly uniform size, the anterior-most pair slightly smaller than the 6 posterior-most pairs, posterior margin concave with a distinct notch, notch depth is 0.1–0.2 posterior width of telson, posterior margin of telson with 6–10 pairs of spines on each side of notch, can be unequally paired. Sample telson spine formulas from the 2005 specimens are 7/8, 6/6, 8/10, 6/6, 7/7, 6/6, and 7/6 on left and right sides of the notch, respectively. Telson overreaching posterior margin of uropods.

Eyes (Fig. 2b, c).—Eyes with cornea imperfectly developed and unafaceted though diffusively pigmented in adults (no juveniles analyzed), but with internal facet-like pattern evident; cornea ovate in outline though fused to each other mesially, and each with small upturned spine on anterodorsal surface.

Antennae (Fig. 2c).—Antennular peduncle reaching distal margin of antennal scale; first article 1.1–1.5 length of second and about 1.9–2.3 length of third, all measured on ventral margin; stylocerite well separated from peduncle, tapering to slender elongate tip variably reaching as far as three-quarters to full length of second article; basal article with dorsolat-

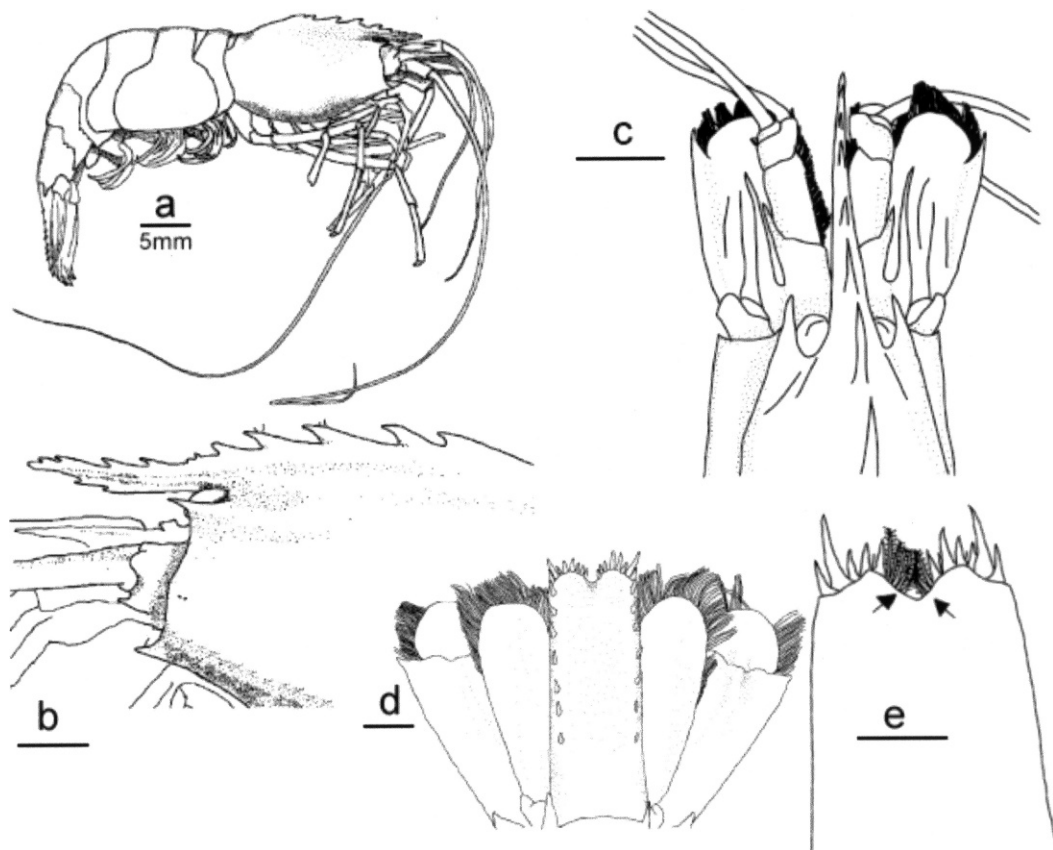


Fig. 2. *Alvinocaris komaii*, holotype female (a–d) and paratype female (e). a, whole specimen, right lateral view; b, rostrum, left lateral view; c, antennular peduncles, dorsal view; d, telson and uropods, dorsal view; e, close-up of posterior margin of paratype telson showing occasional plumose setae. Scale bars: a, 5 mm; b–e, 2 mm.

eral margin extended into strong lateral spine reaching half length of second article and closely appressed to second article, small distal spine ventrally, no obvious distomesial spine; shorter second article with stronger mesiodistal spine. Dorsolateral and ventromesial flagella approximately equal in length, about length of carapace, thickened in basal half. Antennal scale length 1.6–2.3 width, distolateral tooth strong, falling short of broadly rounded distal margin of blade.

Mandible (Fig. 3a, b).—Mandibles similar, with 2-segmented palp, distal segment with long setae on lateral margin and posterior face as illustrated, proximal segment with 4 long, plumose setae on

distolateral margin. Incisor process with an upper portion bearing 1 blunt tooth, lower portion projecting further than upper with 8 sharp teeth, process distinct from incisor process, separated from it by deep notch, rounded tip lacking minute setae.

First maxilla (Fig. 3c, d).—Proximal endite oval, curving anteriorly (dished anteriorly) bearing numerous distal marginal setae, densest around narrow anteromesial tip, armed with teeth on distolateral margin; distal endite with broad base, distal margin curving anteriorly, not armed with teeth, numerous setae on proximal margin and posterior surface, longer plumose setae placed regularly

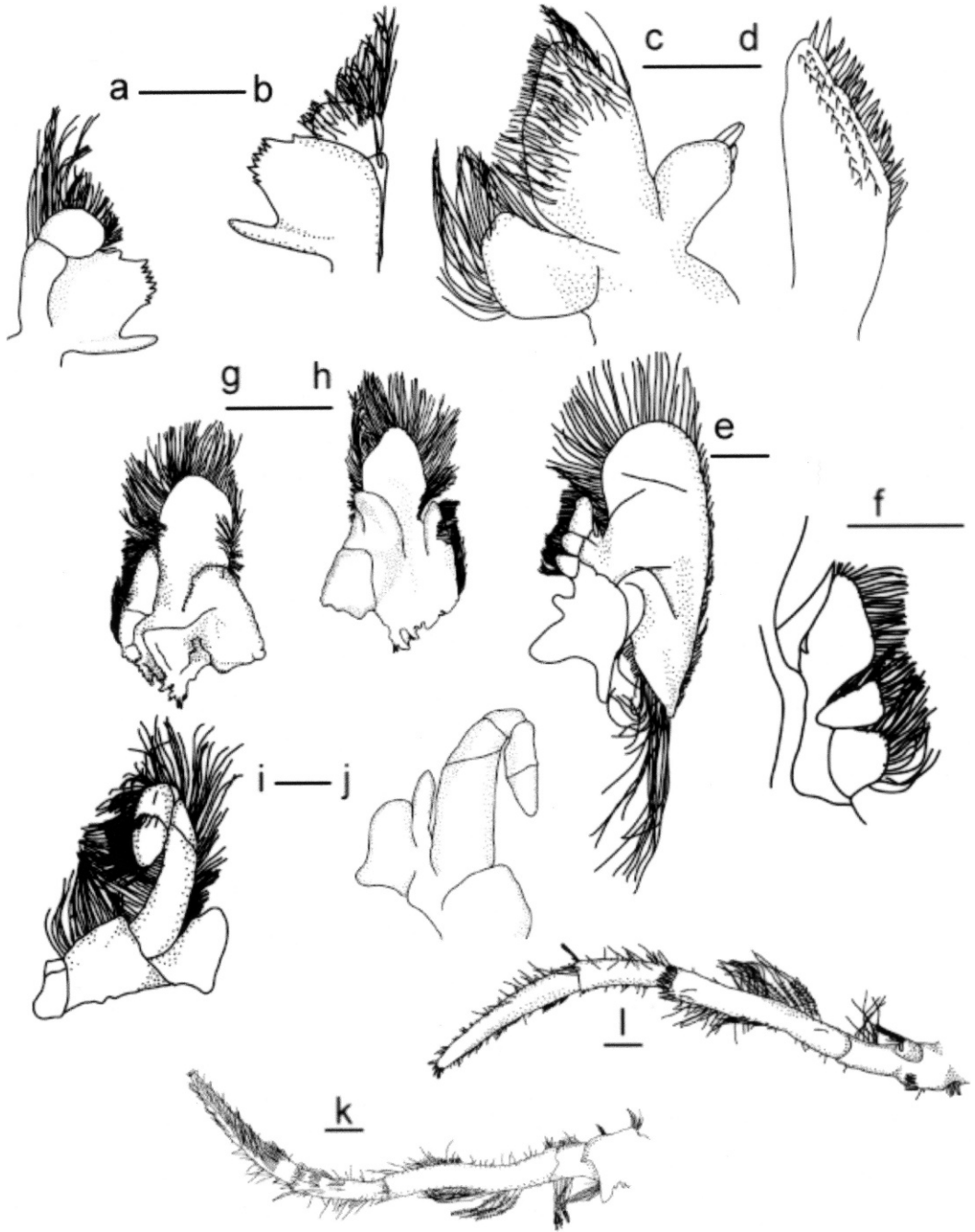


Fig. 3. *Alvinocaris komaii*, holotype female. a, mandible, interior view; b, mandible, exterior view; c, first maxilla, exterior view; d, first maxilla close-up of teeth on distolateral margin of proximal endite; e, second maxilla, interior view; f, second maxilla, interior view; g, first maxilliped, exterior view; h, first maxilliped, interior view; i, second maxilliped, interior view; j, second maxilliped with palp, setae removed, exterior view; k, third maxilliped, ventral view; l, third maxilliped, dorsolateral view. Scale bars: 0.5 mm.

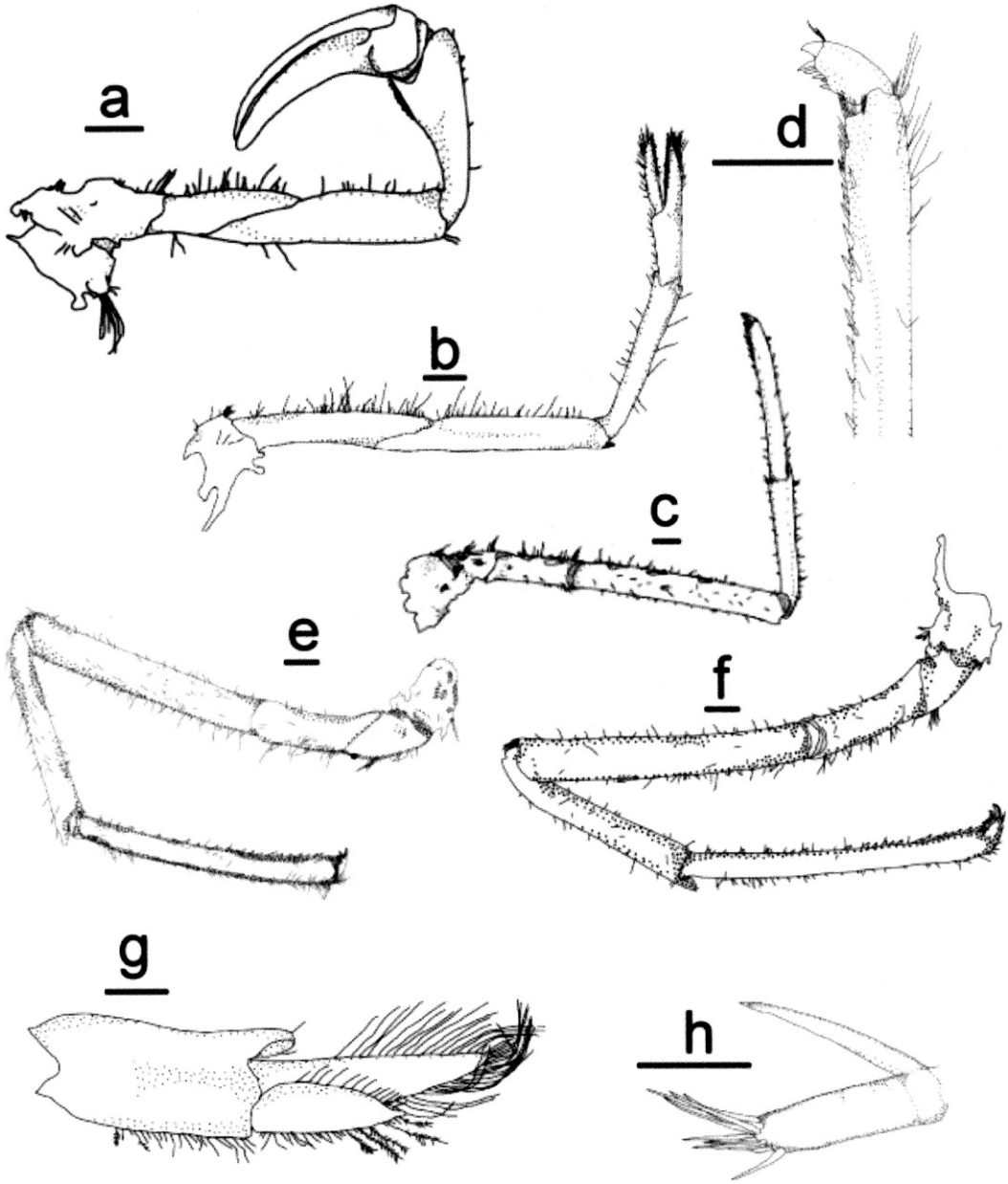


Fig. 4. *Alvinocaris komaii*, holotype female (a–g) and paratype male (h). a, left first pereopod, external view; b, left second pereopod, external view; c, left third pereopod, external view; d, left third pereopod dactylus and carpus, lateral view; e, right fourth pereopod, inner view; f, left fifth pereopod, external view; g, right first pleopod, inner view; h, appendix masculina. Scale bars: 1 mm.

around distal tip and lateral margin of endite; palp with round tip and mesial, subterminal notch without setae.

Second maxilla (Fig. 3e, f).—Endites dished anteriorly, densely setose distally on margins and submarginally, proximal

endite of 2 lobes, distal lobe with small, setose protrusion on anterior margin, distal endite spatulate in posterior view, with uniform row of small setae along lateral margin; palp straight with short row of small, plumose setae on lateral

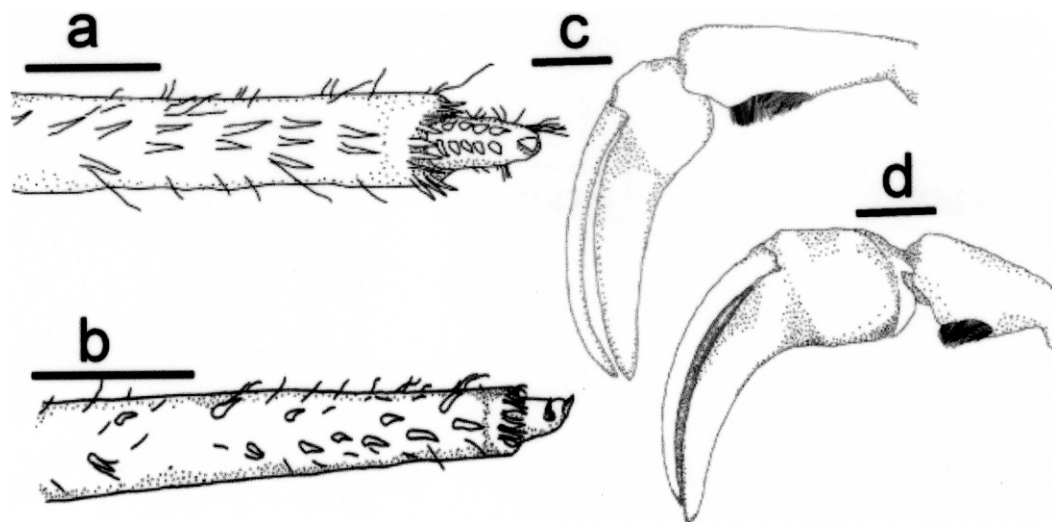


Fig. 5. *Alvinocaris komaii*, holotype female (a, c) and paratype male (b, d). Variation in third pereopod, ventral view (a, b) and chelae of first pereopod (c, d). Scale bars: 1 mm.

margin, tip unarmed; scaphognathite almost rounded anteriorly, fringed with long plumose setae anteriorly, shorter plumose setae on mesial and lateral margins, narrowing to acuminate posterior lobe armed around tip and mesial margin with series of very long, strong setae, row of small setae proximally on mesial margin.

First maxilliped (Fig. 3g, h).—Endite strongly dished anteriorly, fringed along lateral margin by dense setae, along anterior margin by numerous plumose setae; exopod ovate, fringed distally by long plumose setae, submarginal ridge laterally with palp reduced and rounded with setae; epipod bilobed, unarmed.

Second maxilliped (Fig. 3i, j).—Pedi-form but rather flattened; coxa fringed mesially by long, dense, plumose setae, fused basis-ischium with regular mesial row of long, strong, sparsely plumose setae, opposite margin and merus, carpus, propodus bordered by long, plumose setae, dactylus bordered by long plumose or serrate setae, forming particularly dense, nest-like pad around mesial part of dactyl; epipod leaf-like, unarmed; podobranch rudimentary with pointed

tip, mesial branch without terminal seta, no tooth-like projections observed on lateral margin.

Third maxilliped (Fig. 3k, l).—Long, 4-segmented, reaching as far as distal end of antennal scale; terminal segment triangular in cross-section, tapered distally, tip with 2 spines and additional setae, an irregular row of about 4 additional spines subterminally on mesial face, 5 groups of distally directed serrate setae arranged in close-set, transverse tracts along mesial face, groups overlapping to form a longitudinal pad; posterolateral face of terminal segment somewhat dished, angle between posterolateral and anterolateral faces armed with row of 7 or 8 slender spines or spine-like setae; carpus with pads of dense setae on distal two-thirds, similar and adjacent to those of terminal segment; merus-ischium with row of long, plumose setae, otherwise armed as illustrated; coxa with small epipod, with tuft of long, plumose setae at junction.

First pereopod (P1, Figs. 4a, 5c, d).—Reach to half the length of terminal segment on third maxilliped, robust; fingers curved downwards and outwards, together concave laterally, fixed finger

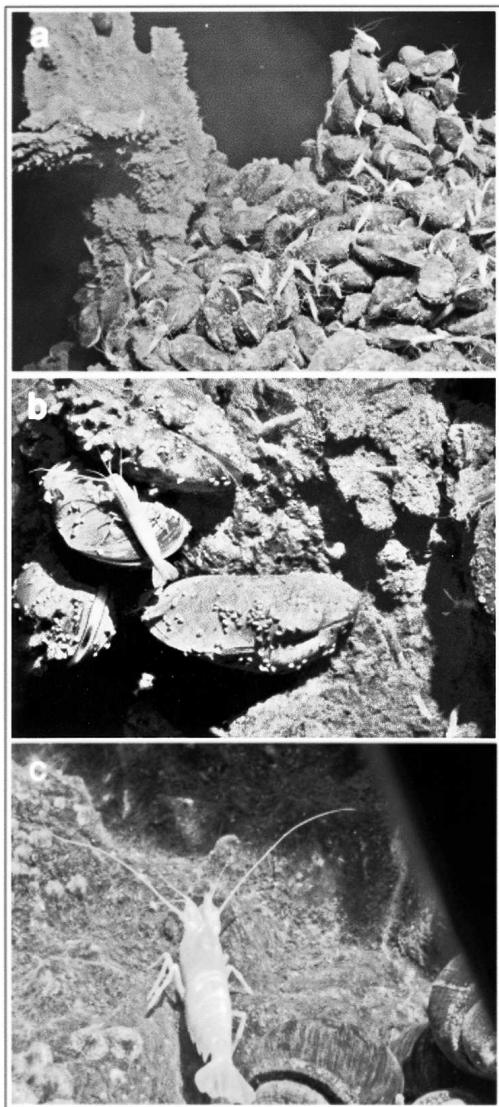


Fig. 6. In-situ photographs of *Alvinocarididae* from the ABE site. a, several *A. komaii* on top of mussel *Bathymodiolus brevior* on chimney wall; b, closer view on *B. brevior* (note the presence of limpet *Lepetodrilus schrolli* and barnacle *Eochionelasmus ohtai* on shells); other alvinocaridids, either *Nautilocaris saintlaurentae* or *Chorocaris vandoverae*, present on right side of photo on bare substrate; c, on bare substrate, note gastropod *Ifremeria nautili* below and barnacles *E. ohtai* to left on bare substrate.

twice the width of dactyl basally, opposing edges of fingers each armed with row of minute uniform teeth close-set against one another, teeth on dactyl somewhat

longer than on fixed finger, row on dactyl angled towards convex side to interdigitate with teeth on fixed finger, finger tips slightly spooned by teeth fanned around edge, latter teeth fused to form corneous edge around lateral border of dactyl tip, line of sensory setae on moving finger's concave surface running parallel to teeth, setae on fixed finger not obvious; dactyl fractionally outreaching fixed finger, palm half the length of finger in female and same length in males; carpus short, cone-shaped, cupped distally to accommodate palm, with smaller blunt protuberance on distomesial margin, lateral ridge produced distally into strong process with pinched tip (process slender, acuminate in female paratype); dense, clearly delineated pad of strong, serrate setae posteriorly between pinched and smaller process; merus, ischium somewhat flattened, they and distinct basis and coxa armed as illustrated.

Second pereopod (P2, Fig. 4b).—Shorter and more slender than first, reaching half length of antennal scale; fingers subequal to palm, similar in size and shape, opposing edges without gap, each pectinate with single row of short teeth directed obliquely distally, row beginning about 0.2 from base of dactyl, fixed finger has teeth all its length increasing slightly in size distally, terminating in larger spine at each finger tip, terminal spines cross when chela is closed, with 2 tufts of long setae on dactyl; carpus, merus armed as illustrated, ischium with single spine at about three-quarters length (1 individual showed 2 spines on one side).

Third to fifth pereopods (P3–P5, Figs. 4c–f, 5a, b).—Similar in length although merus becomes progressively shorter from the P3 to P5 and propodus longer, P3 outreaching antennal scale by 0.5 propodus; dactyls short, armed with single corneous spine and single accessory spinule in holotype, 2 rows of 4 or 5 accessory spinules in paratypes on flexor surface, smallest proximally, longest dis-

tally; propodus with irregular, composite row of spines ventrolaterally becoming denser distally, row shortest and sparsest on P3, longest and densest on P5; carpus of each pereopod with distodorsal extension over proximal extensor surface of propodus; ischium and merus of P3 stronger than in P4 and P5, meri of pereopods with 3 spines on P3 and P4, without spines on P5, ischium of pereopods armed with 2 posteroventral spines on P3 and P4, none or 1 on P5.

Pleopods (Fig. 4g, h).—Well developed, endopods about half length of exopod on first pleopod, subequal with exopod in pleopods 2–5; appendix interna of pleopods 2–4 well developed and smooth, of pleopod 5 twice as wide, parallel-sided, with 30–50 cincinnuli distributed in fingernail-shaped pad at tip on mesial surface; appendix masculina with approximately 8 slender spines around tip and subterminally.

Uropods (Fig. 2d).—With exopod and endopod subequal, slightly shorter than telson, exopod with movable spine mesial to distolateral tooth half its length; diaresis sinuous.

Etymology.—Named in honor of Dr. Tomoyuki Komai of the Natural History Museum and Institute in Chiba, Japan, for his significant contributions to the taxonomy of the Alvinocarididae.

Variation.—There are no significant differences between males and females with regard to any of the examined characters (dorsal and ventral rostral teeth numbers, abdominal pleuron (3–5) spine numbers, telson dorsolateral spine and posterior marginal spine number) or measurements (carapace length, carapace width, total body length, rostral length, telson length and anterior/posterior widths, antennal scale length and width, pereopod 1 palm width and height, pereopod 3 carpus, merus and propodus lengths and antennal peduncle segment (1–3) lengths and widths) ($p > 0.08$). It should be noted that very few males were

collected (9 out of 45 individuals with intact second pleopods). An increased number of individuals may reveal patterns in the ratio of pereopod 1 palm width to height and the ratio of propodus length to carpus length. Though Webber (2004) found dimorphic variation between the sexes in *Alvinocaris niwa*, Kikuchi & Ohta (1995) observed that variation in the first pereopod chelae of *A. longirostris* corresponded to increase in carapace length and between the left and right chelae of a single individual. Additionally, variation in the overall appearance of the first pereopod chelae has been noted for the genus in general (Komai & Segonzac 2005), *A. methanophila* (Komai et al., 2005) and in other alvinocaridids: *Chorocaris paulexa* (Martin & Shank, 2005) and *Opaepele susannae* (Komai et al., 2007). On the other hand, distinct variation in the first pereopod chelae was not observed in *Shinkaicaris leurokolos* (Komai & Segonzac, 2005).

Individuals of *Alvinocaris komaii* collected from ABE appear to be more robust than those collected from KM. Because there were 3 individuals from TC that consisted only of the anterior portion of the animal (no pleopods or telson), only ABE and KM collections are compared. There was no difference in rostral armature, but rostral length was significantly longer for specimens from ABE ($p \leq 0.001$). *Alvinocaris komaii* from ABE also have larger ratios of rostral length to carapace length ($p < 0.001$), though carapace length was not significantly different between sites ($p = 0.12$). Hence, rostra of ABE individuals are larger irrespective of body size, yet this trend appears to be driven by 4 out of 7 individuals collected at ABE. The first segment of the antennular peduncle is longer in ABE individuals ($p = 0.001$) as is the ratio of the first segment to the third segment of the antennular peduncle ($p = 0.002$). Palm width, height, and the ratio of width to height are also larger among

individuals from ABE than from KM ($p < 0.02$). In conclusion, individuals from our collections at ABE may appear proportionally larger than those from the KM collections, but disproportionately have longer rostra and antennular peduncles than KM individuals (see Table 1). It should be noted that sample sizes of individuals collected at ABE are low and it may be premature to extend this observation to the population level at this particular site.

Ecology.—*Alvinocaris komaii* was observed at four of the six study sites targeted by the Ridge2000 ELSC Integrated Study Site. We first discovered this species in the 2005 expedition in quantitative whole-community collections from KM, where it occurs in great abundance. During the 2006 expedition, *A. komaii* was discovered at TC, ABE, and TM in addition to KM (Fig. 1). The depth spans from 1880 m in the southern-most site, TM, to 2720 m in the northern-most sites, KM and TC. At each of these sites, it co-occurs with the alvinocaridids *Nautilocaris saintlaurentae* and *Chorocaris vandoverae*. A hippolytid, *Lebbeus* sp. nov. (Michel Segonzac pers. comm.), also occurs at ELSC. Despite being documented on and near the mussel *Bathymodiolus brevior* von Cosel, Métevier & Hashimoto, 1994, *Lebbeus* sp. nov. typically inhabits the communities along the periphery of the vent, whereas the three alvinocaridids inhabit the communities directly influenced by hydrothermal discharge.

Most commonly, *A. komaii* is seen on top of beds composed of the chemoautotrophic mussel, *B. brevior* (Fig. 6a, b). This habitat is common among alvinocaridid shrimp, though some species are seen exclusively on hydrothermal chimneys (i.e., *Rimicaris*) or utilize both the geologic and biologic substrate. Video records show *A. komaii* making relatively few excursions into beds of the chemoautotrophic snail, *Ifremeria nautiliei* Bouchet

& Warén, 1991, as well on the bare rock of hydrothermal chimneys (Fig. 6c). On rare occasion, *A. komaii* was observed in beds of the provannid snail *Alviniconcha hessleri* Okutani & Ohta, 1988. Other fauna found in association with *A. komaii* include the decapod crabs *Austinograea alayseae* Guinot, 1989, *Austinograea williamsi* Hessler & Martin, 1989, and *Paralomis hirtella* de Saint Laurent & MacPherson, 1997; the barnacle *Eochionelasmus ohtai* Yamaguchi & Newman, 1990; the gastropods *Desbruyeresia cancellata* Warén & Bouchet, 1993, *Lepetodrilus schrolli* Beck, 1993 and *Olgasolaris tollmanni* Beck, 1992; and the polychaetous annelids *Archinome* sp. and *Opisthotrochopodus trifurcus* Miura & Desbruyères, 1995.

Alvinocaridids are typically described as either primary consumers or necrophagous (Segonzac et al. 1993). Video imagery documented *A. komaii* feeding on the verrucamorph barnacle, *E. ohtai*, which was crushed incidentally by the submersible. *Eochionelasmus ohtai* co-occurs with *A. komaii* as it frequently colonizes the shells of *B. brevior*. Additionally, *A. komaii* was observed on rock covered in bacteria and barnacles. We have not observed *A. komaii* directly feeding on the mussels. It is likely that this shrimp species is a generalist, feeding from several potential pools including grazing bacteria from bare rock and mussel shells and feeding opportunistically on other sessile fauna or necrotic material. The diet of the new species is uninvestigated.

Little can be ascertained about the reproductive biology of *A. komaii* from these individuals. Though our collections were haphazard (specimens come from intact community collections for ecological analyses, targeted for suction sampler or as bycatch in other collections of snails and mussels) and not quantitative, there appears to be a sex-ratio skew in favor of females. This skew has been noted for

Table 1.—Characters of *Ahinocaris* species from the Pacific Ocean. l = length, w = width, h = height.

Character	<i>A. brevitelsonis</i>		<i>A. dissimilis</i>		<i>A. longirostris</i>		<i>A. lasca</i>		<i>A. niwa</i>		<i>A. komati</i>	
	Kikuchi & Hashimoto 2000	Kikuchi & Segonzac 2005	Komai & Segonzac 2005	Kikuchi & Ohta 1995	Williams & Chace 1982	Webber 2004 ^a	This Study					
Locality ^a	OT	OT	OT	NZ, OT, SB	EPR, GR	NZ	LB					
Carapace w/l	0.7	0.65–0.8	0.65–0.72	0.65–0.72	0.55–0.67	N/A	0.53–0.7					
Pterygostomian tooth	weak	weak	strong	strong	weak	strong	strong					
2nd segment antennular peduncle l/w	1.8	1.43–1.78	1.58–1.69	1.58–1.69	2–2.2	1.86	1.43–2.25					
Antennal scale l/w	1.87	1.9–2.16	1.72–1.9	1.72–1.9	2.2–2.6	1.7	2					
Antennal scale l/Carapace l	0.55	0.48–0.52	0.5	0.5	0.5	0.69	0.43–0.48					
Rostrum l/Carapace l	13	0.53–0.61	0.64–0.98	0.64–0.98	0.6–0.7	0.24 ^b	0.33–0.92					
Dorsal teeth	7	13–17	9–15	9–15	10–14	5–17	9–12					
Ventral teeth	end of 2nd segment	1–2	4–9	4–9	3–4	0–1	2–6					
Rostrum reaches	unarmed	end of 2nd segment	2nd and 3rd segments	2nd and 3rd segments	beyond 3rd segment	end of 1st segment	2nd and 3rd segments					
3rd pleuron spines	unarmed	unarmed	unarmed or few “denticles”	unarmed or few “denticles”	unarmed	0–1	0–3					
6th somite l/h	1.4	1.3–1.4	1.5–1.7	1.5–1.7	1.5–1.7	1.4	1.17–1.87					
Telson dorsolateral spines	6–7	5–8	5–7	5–7	7–9	4–11	7					
Telson postermarginal spines	6 pairs	2 pairs	2	2	6–9 pairs	2 pairs	6–10 pairs					
Telson postermarginal setae	2 pairs	12–14	12–14	12–14	0 ^d	14–29	0 ^d					
Telson reach to uropod	<	<	< to at margin	< to at margin	< to slightly > margin	<	>					
Telson l/anterior w	2.7	2.7–2.9	2.53–2.8	2.53–2.8	3.2–3.3	2.96	2.4–2.9					
Telson l/posterior w	4.3	4.3–4.6	4.1–4.9	4.1–4.9	4.1–4.3	2.12	2.9–3.3					
Pereopod 1 palm l/h	2.08	2.5	2.5	2.5	1.26	1.29	0.63–1.68					
Pereopod 1 dactylus	< palm	> palm	> palm	> palm	> palm	< palm	> palm					
Pereopod 3 carpus l/Propodus 1	0.68	0.6–0.65	0.6–0.65	0.6–0.65	0.7–0.75	0.8	0.66–0.88					
Pereopod 3 merus l/h	7.3	6.4	6–6.4	6–6.4	8	5.76	6.0–8.4					

^a EPR = East Pacific Rise; GR = Galapagos Rift; LB = Lau Basin; NZ = New Zealand; OT = Okinawa Trough; SB = Sagami Bay.

^b Ratios are derived from measurements taken on drawings.

^c Only from male holotype and female paratype.

^d 1–6 setae are on rare occasion observed.

Alvinocaris muricola off the West African Margin, Gulf of Guinea (Ramirez-Llodra & Segonzac 2006). We have not observed gravid females, or females carrying egg masses between their pleopods, in any video we have viewed from June 2005 or September 2006. Fertilization and copulation of *A. komaii* follows typical courtship observed among caridean shrimp (Tyler & Young 1999). One instance of courtship was observed during the September 2006 cruise (video available upon request from corresponding author). Courtship was commenced when one individual nudged into another on the substrate (shell of *B. brevior*). The nudged individual grasped the other's carapace with pereopods 2 and 3. Both individuals then faced each other ventrally and moved into the water column where copulation took place immediately. Both individuals then swam together back to the substrate (shell of *B. brevior*) about 10 cm from the starting point. Since a copulation event was observed in September, it is plausible that the development period for embryos is during November to December. More collections at other times of the year would be needed to discern the reproductively active period of *A. komaii*. Individuals of *Chorocaris vandoverae* that were collected and observed from the same locations as *A. komaii* have been observed to be gravid both in June 2005 and September 2006.

Molecular Phylogeny.—The molecular phylogeny of the Alvinocarididae based on the COI sequence shows that *A. komaii* is genetically distinct from all other species available in the databases and from *A. muricola* (Gulf of Mexico and REGAB, Fig. 7). The *Mirocaris* group forms a very well supported monophyletic group, apart from the *Alvinocaris/Opaepele/Rimicaris/Chorocaris* clade. In this latter group, the sequence referred to as “Alvinocarididae Blake Ridge” probably corresponds to *Alvinocaris methanophila* Komai, Shank, & Van

Dover, 2005 (see Van Dover et al. 2003), the second species collected from that locality with *A. muricola*. It appears clear that *Alvinocaris* is polyphyletic and that *A. komaii* belongs to the *Alvinocaris/Opaepele/Rimicaris/Chorocaris* clade. In that clade, the position of *A. komaii* is uncertain, as the bootstrap value is only 39.7%.

Discussion

Morphological affinities.—*Alvinocaris komaii* is characterized from all known *Alvinocaris* by two apomorphic characters: a distinctive notch in the telson and 2 rows of accessory spinules of the dactyli of pereopods 3–5. *Alvinocaris lusca* Williams & Chace, 1982 and *A. dissimilis* Komai & Segonzac, 2005, are reported to be very shallowly notched. The notch in *A. dissimilis* is a more rare occurrence (Komai & Segonzac 2005). In comparison to *A. komaii*, the notch in *A. lusca* is shallow and can vary from more of a sinusoidal edge to a distinct shallow notch in some individuals. The posterior margin of the third abdominal pleuron of *A. lusca* is reported to be unarmed (Komai & Segonzac 2005, Williams & Chace 1982), but 35 out of 43 individuals of *A. komaii* with intact abdominal pleura had at least 1 distinct marginal spine on at least 1 side of the third pleuron (Table 1). In *A. komaii*, this is a highly variable character. Marginal spines on the fourth and fifth abdominal pleurae are shown to be highly variable within and between species (Table 1; Komai & Segonzac 2005). *Alvinocaris komaii* is further separated from *A. lusca* by the following suite of characters: strong pterygostomian tooth, shorter antennal scale, lower telson length to width ratios posteriorly and anteriorly, and a somewhat shorter reach of the rostrum (Table 1).

Alvinocaris brevistelsonis Kikuchi & Hashimoto, 2000 was described from the Okinawa Trough. *Alvinocaris brevistelso-*

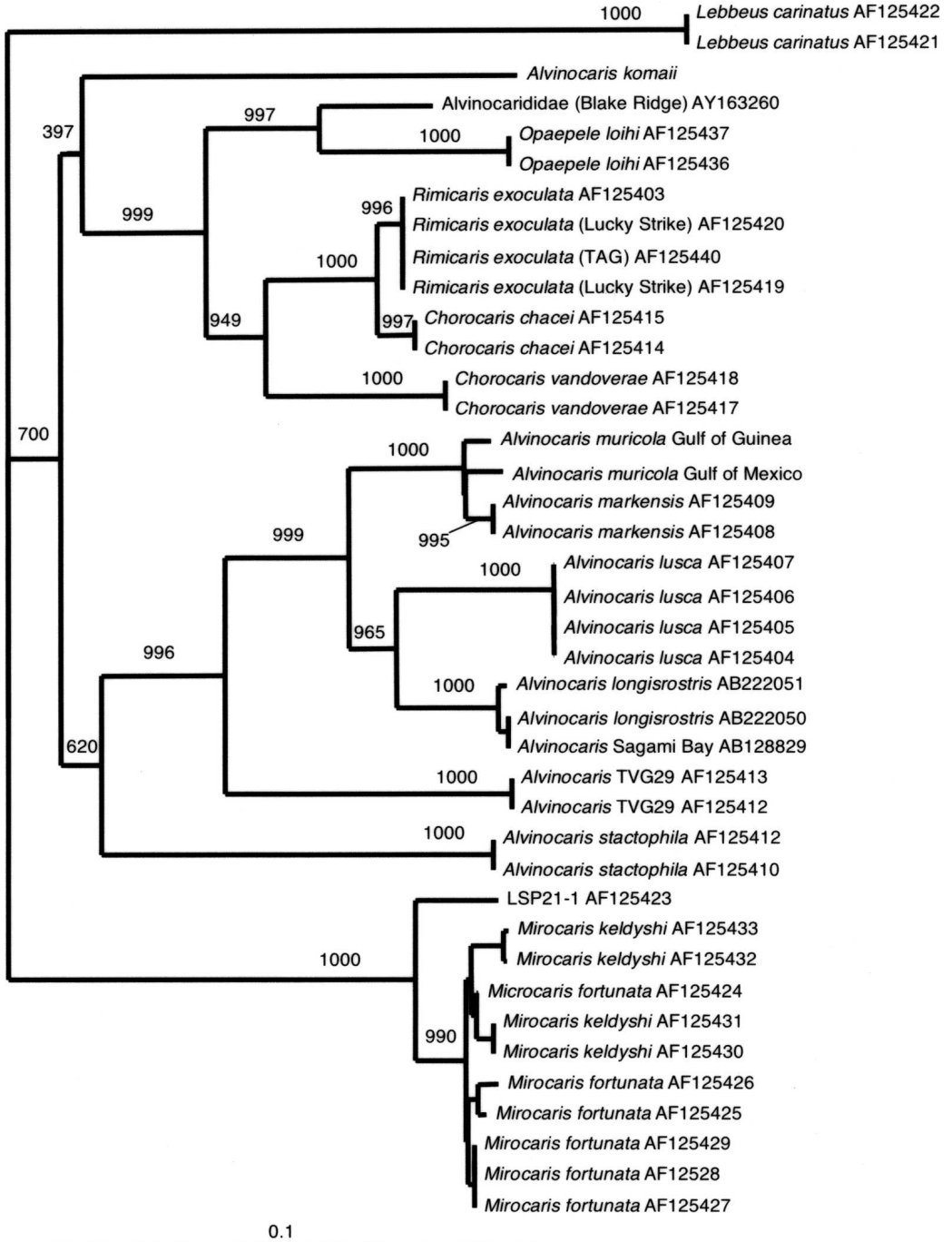


Fig. 7. Phylogenetic tree of the Alvinocarididae based on 600-bp alignment of partial COI sequence. *Lebbeus carinatus* used as outgroup. All GenBank accession numbers appear after species names. Bootstrap values given for branches. Arrow points at position of *Alvinocaris komai*.

nis is only known from the holotype (see Komai & Segonzac 2005 for discussion) and differs from *A. komaii* in having a weak pterygostomial tooth, a convex posterior margin of the telson that is shorter than the uropod margin, larger ratio of telson length to posterior width, and a larger ratio of length to height of pereopod 1 palm (Table 1). *Alvinocaris brevistelsonis* is further distinguished from *A. komaii* by having 2 pairs of posteromarginal plumose setae. Plumose setae are sometimes present on the posterior telson margin in *A. komaii*, but appear to represent an abnormality and can be variable in number (Fig. 2d, e). All other species of *Alvinocaris* are markedly different from *A. komaii* (see Table 1 for comparison of Pacific Ocean species and Komai & Segonzac 2005 for a detailed analysis of the genus).

Several undescribed specimens of *Alvinocaris* are mentioned in previous papers. Desbruyères et al. (1994) described the initial ecology of the North Fiji and Lau back-arc basins. In their paper, they refer to "*Alvinocaris* sp." (also referred to as *Alvinocaris* sp. D in Martin & Haney 2005) living on mussel beds at 2 sites at the Lau Basin, Hine Hina and Vai Lili, which were not visited during the expeditions that collected our specimens. It is likely that the species referred to as "*Alvinocaris* sp." in Desbruyères et al. (1994) is *A. komaii*, but it should be noted that another alvinocaridid shrimp was later described by Komai & Segonzac (2004) from the North Fiji and Lau back-arc basins as a new genus and species: *Nautilocaris saintlaurentae*. However, adults of *A. komaii* and *N. saintlaurentae* are markedly different and easy to distinguish from photograph or video imagery. Komai & Segonzac (2004) mentioned an undescribed species of *Alvinocaris* from the ELSC and noted it was distinguishable from *N. saintlaurentae* and *Chorocaris vandoverae* by its "well-developed rostrum and the red color of the cepha-

lothorax." Komai & Segonzac (2005) also noted the affinity of this *Alvinocaris* species from the Lau Basin to an undescribed species in the Bismarck Sea. It is unclear whether *A. komaii* represents this species, but our extensive survey of the vent communities at 4 sites along the ELSC resulted in no other undescribed alvinocaridid. To date we have found no other description of an *Alvinocaris* resembling *A. komaii* as described in this study.

Phylogenetic affinities.—The phylogenetic tree, based upon 600 bp of the mitochondrial COI nucleotide concurs with earlier molecular phylogenetic work of the family (Shank et al. 1999). There are distinct *Opaepele/Chorocaris/Rimicaris* (*O/C/R*), *Alvinocaris* and *Mirocaris* clades with well-supported bootstrap values. With the addition of *A. komaii*, deeper branching patterns between the *Alvinocaris* and the *O/C/R* clades remain unclear. Although *A. komaii* seems to cluster with the *O/C/R* clade and not the monophyletic *Alvinocaris* clade, this is supported by low bootstrap values (39.7%). Increased sampling of genes and taxa are needed to distinguish inter-generic relationships within the Alvinocarididae.

Our phylogeny agrees with the earlier phylogenetic work of Shank et al. (1999) and the revision of the genus *Alvinocaris* by Komai & Segonzac (2005) in that geography appears to play little role in shaping Alvinocarididae phylogeny. Clustering appears to be consistent with morphology. The *Mirocaris* clade is molecularly distinct from the *O/C/R* and *Alvinocaris* clades and species share the presence of "strap-like" epipods on the third maxilliped and pereopods 1–4.

Nautilocaris saintlaurentae is also described as having epipods on the third maxilliped and pereopods 1–4 (Komai & Segonzac 2004), a character potentially grouping it with the *Mirocaris* clade. *Nautilocaris saintlaurentae* also has a laterally-compressed, dentate rostrum, a plesiomorphic character in common with

the *Alvinocaris* clade. We hypothesize that *N. saintlaurentae* should occupy a position basal to the *Mirocaris* clade if the presence of the epipods is a synapomorphy of that clade. The *Alvinocaris* clade is composed of individuals with typical *Alvinocaris* morphology: a laterally compressed, dentate rostrum, lack of epipods on the third maxilliped and pereopods 1–4, dorsolateral spines on telson arranged linearly, acuminate antennal tooth, 1 or 2 rows of accessory spinules on dactyli of pereopods 3–5. Members of the *O/C/R* clade share the absence of epipods on the third maxilliped and pereopods 1–4, acuminate antennal spine, and 1 or 2 rows of spines on dactyli of pereopods 3–5 with the *Alvinocaris* clade but differ in having a nonlinear arrangement of dorsolateral spines on the telson and a dorsoventrally compressed, triangular rostrum lacking dentation. *Opaepele loihi* has minute inconspicuous dentation while *O. susannae* lacks any remnant of dentation and more closely resembles the *Chorocaris/Rimicaris* clade (Komai et al. 2007). *Alvinocaris komaii* has all the characteristics of belonging to the *Alvinocaris* clade and lacks the rostral and telson characters defining the *O/C/R* clade. It is unclear why *A. komaii* groups with the *O/C/R* clade, but the low bootstrap value shows this grouping lacks statistical support. The presence of 2 rows or accessory spinules may suggest a closer affinity to a clade composed *A. niwal* *Shinkaicaris* plus the *O/C/R* clade.

Dichotomous key to the known species of the Alvinocarididae

1. Rostrum ridged, compressed dorso-laterally, armed with teeth dorsally, sometimes ventrally 2
 - Rostrum broadly rounded dorsally or faintly ridged, unarmed or with rudimentary denticles on the dorsal surface, triangular, flattened dorso-ventrally 14
2. Antennal tooth distinctly buttressed, telson dorsolateral spines arranged in a sinusoidal row, more than 2 rows of spines on dactyli of pereopods 3–5 *Shinkaicaris leurokolos* (Kikuchi & Hashimoto, 2000) [Minami-Ensei Knoll, Okinawa Trough, 705 m]
 - Antennal tooth not buttressed, telson dorsolateral spines not distinctly arranged in a sinusoidal row, 1 or 2 rows of accessory spinules on dactyli of pereopods 3–5 3
3. Third maxilliped to fourth pereopod with strap-like, terminally hooked epipods, telson with 7–9 dorsolateral spines arranged in slightly sinusoidal row and with 12–19 spines on posterior margin *Nautilocaris saintlaurentae* Komai & Segonzac, 2004 [North Fiji and Lau Back-Arc Basins, 1700–2700 m]
 - No strap-like epipods present on third maxilliped to fourth pereopod, dorso-lateral spines on telson arranged in a straight row *Alvinocaris* 4
4. Posterior margin of telson with more than 2 pairs of spines 5
 - Posterior margin of telson with 2 pairs of spines at lateral corners and 10–16 plumose setae 8
5. Posterior margin of telson with mesial spines of subequal length, lacking plumose setae mesially; ventral margin of rostrum with 1 tiny tooth
 - .. *A. stactophila* Williams, 1988 [Upper Louisiana Slope, Gulf of Mexico, 534 m]
 - Ventral margin of rostrum with 2 or more teeth; posterior margin of telson with mesial spines of greatly unequal length and 1 to 3 mesial pairs of short plumose setae 6
6. Rostrum with more than 5 ventral teeth; telson posterior margin convex with 6 pairs spines and 1 pair mesial setae, less than posterior margin of uropod
 - *A. brevitelsonis* Kikuchi & Hashimoto, 2000 [Minami-Ensei Knoll, Okinawa Trough, 705 m]
 - Rostrum 6 or less teeth; telson posterior margin slightly sinusoidal or concave mesially (i.e., notched appearance) and at or greater than the posterior margin of uropod 7

7. Antennal scale 2.2–2.6 times longer than wide; telson posterior margin slightly sinusoidal to shallowly concave (i.e., notched) *A. lusca* Williams & Chace, 1982 [Galápagos Rift, 9°N East Pacific Rise, 2400–2600 m]
- Antennal scale 1.6–2.1 times longer than wide; telson distinctly concave (i.e., notched) mesially; stylocerite reaching second antennular peduncle segment *A. komaii* (This Study) [Eastern-Lau Spreading Center, 1800–2700 m]
8. Rostrum usually unarmed on ventral margin 9
- Rostrum always armed on ventral margin 10
9. Second segment of antennular peduncle about 1.1–1.2 times as long as wide; telson length 2.2–2.5 times as long wide anteriorly
 *A. williamsi* Shank & Martin, 2003 [Menez Gwen, Mid-Atlantic Ridge, 850 m]
- Second segment of antennular peduncle about 1.8 times as long as wide; telson length about 2.9 times as long as wide anteriorly
 *A. niwa* Webber, 2004 [New Zealand volcanic seamounts, 367–1346 m]
10. Rostrum with less than 3 ventral teeth; pterygostomial tooth not strongly produced anteriorly; second segment of antennular peduncle 1.4–1.5 times longer than wide
 *A. dissimilis* Komai & Segonzac, 2005 [Minami Ensei Knoll, Okinawa Trough, 705 m]
- Rostrum usually with more than 3 ventral teeth; pterygostomial tooth of carapace strongly produced anteriorly; distolateral tooth of antennal scale usually with straight mesial margin 11
11. Anterior part of branchial region somewhat inflated, strongly convex; post-antennal groove deep; telson length greater than 2.9 telson anterior width 12
- Anterior part of branchial region not particularly inflated, only slightly convex; post-antennal groove shallow; telson length less than 2.9 telson anterior width 13
12. Telson at or greater than posterior margin of uropod; posterior-most tooth of dorsal rostral series arising from 0.34–0.40 of carapace length; second segment of antennular peduncle 1.9–2.1 times longer than wide; antennal scale 1.9–2.1 times longer than wide
 *A. muricola* Williams, 1988 [Florida Escarpment, Gulf of Mexico, 3277 m; Barbados Accretionary Prism, 1697 m; West Equatorial African Margin, 3150 m]
- Telson slightly less than posterior margin of uropod; posterior-most tooth of dorsal rostral series arising from 0.21–0.34 of carapace length; second segment of antennular peduncle 1.35–1.95 times longer than wide; antennal scale 1.7–1.85 times longer than wide *A. methanophila* Komai, Shank, & Van Dover, 2005 [Blake Ridge Diapir, 2155–2167 m]
13. Rostrum usually not reaching distal margin of antennular peduncle; posterior-most tooth of dorsal rostral series arising from 0.24–0.31 of carapace length; second segment of antennular peduncle 1.8–2.05 times longer than wide; antennal scale 1.91–2.04 times longer than wide *A. markensis* Williams, 1988 [Lucky Strike to Ashadze, Mid-Atlantic Ridge, 1693–3650 m]
- Rostrum reaching or overreaching distal margin of antennular peduncle, posterior-most tooth of dorsal rostral series arising from 0.38–0.48 of carapace length; second segment of antennular peduncle 1.58–1.69 times longer than wide; antennal scale 1.72–1.9 times longer than wide *A. longirostris* Kikuchi & Ohta, 1995 [Okinawa Trough, 1053–1627 m; Off Hatsushima site, Sagami Bay, 1120–1220 m; Brothers Caldera, New Zealand, 1196–1810 m]
14. Antennal scale, bases of antennae, and stylocerite closely approximated, forming opercular complex shielding mouthparts; carapace greatly inflated with dorsal “eyespot”; rostrum greatly reduced; eyes greatly modified, forming ocular plate *Rimicaris* 15
- Antennal scale, bases of antennae, and stylocerite not closely approximated; carapace not greatly inflated; rostrum reduced but distinct; ocular

- plates fused mesially, but not forming ocular plate 16
15. Carapace without setae *Rimicaris kairei* Watabe & Hashimoto, 2002 [Kairei Field, Central Indian Ridge, 2454 m]
- Carpace ornamented with tufts of setae *Rimicaris exoculata* Williams & Rona, 1986 [TAG, Mid-Atlantic Ridge, 3620–3650 m]
16. Strap-like epipods on third maxilliped and pereopods 1–4 *Mirocaris* 17
- No strap-like epipods on third maxilliped and pereopods 18
17. Submarginal setae on faces of fingers on first chelae *Mirocaris fortunata* Martin & Christiansen, 1995 [14°N–38°N, Mid-Atlantic Ridge, 850–3650 m]
- No submarginal setae on faces of fingers on first chelae *Mirocaris indica* Komai, Martin, Zala, Tsuchida, & Hashimoto, 2006 [Central Indian Ridge, 2422–3300 m]
18. Rostrum with minute ‘denticles’ or unarmed, outer ramus of uropod with 1 movable spine at posterodistal corner *Opaepele* 21
- Rostrum without teeth, terminating bluntly; outer ramus of uropod with 2 movable spines posterodistal corner *Chorocaris* 19
19. Branchiostegal angle of carapace unpronounced, nearly straight; rostrum reaching but not exceeding postorbital prominences *Chorocaris chacei* (Williams & Rona, 1986) [14°N–38°N, Mid-Atlantic Ridge, 850–3650 m]
- Branchiostegal angle of carapace rising from about 30° from horizontal; rostrum clearly exceeding postorbital prominences 20
20. Anterolateral tooth of antennal scale reduced, blunt, following lateral margin of antennal scale *Chorocaris vando-verae* Martin & Hessler, 1990 [Mariana, 3595–3660 m; Lau Basin, 1750–2750 m]
- Anterolateral tooth of antennal scale acute, directed forward and laterally away from margin of antennal scale *Chorocaris paulexi* Martin & Shank, 2005 [South East Pacific Rise, 2573–2832 m]
21. Rostrum armed with up to 6 minute denticles dorsally, weakly carinate dor-

- sally, tip acuminate
 *Opaepele loihi* Williams & Dobbs, 1995 [Loihi Seamount, Hawaii, 980 m]
- Rostrum unarmed, without dorsal carina, tip rounded or subtruncate *Opaepele susannae* Komai, Giere & Segonzac, 2007 [South Mid-Atlantic Ridge 4°–10°S, 1500–2986 m]

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