# 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*

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#### Abstract

The caridean shrimp genus Alvinocaris Williams and Chace, 1982 (Bresilioidea: Alvinocarididae) is revised based upon type material and newly obtained samples from various reducing environments of the deep-sea floor of the world. All species are known from chemosynthetic communities associated with hydrothermal vents, brine or cold seeps. Eight named species are recognized in Alvinocaris, of which one is new, A. dissimilis sp. nov. from the hydrothermally influenced area of Minami-Ensei Knoll, Mid-Okinawa Trough. Alvinocaris dissimilis sp. nov. was confused with A. brevitelsonis in the original description of the latter species by Kikuchi and Hashimoto (2000). Seven previously described species (A. lusca Williams and Chace, 1982, A. markensis Williams, 1988, A. muricola Williams, 1988, A. stactophila Williams, 1988, A. longirostris Kikuchi and Ohta, 1995, A. brevitelsonis Kikuchi and Hashimoto, 2000, and A. williamsi Shank and Martin, 2003) are re-described, and characters distinguishing these species are re-assessed. Two species are confounded in the type series of A. stactophila Williams, 1988. The taxonomic status of the allotype of A. stactophila was not satisfactorily determined, as it appears to be an immature specimen. The geographic range of A. muricola, previously known only from cold seeps on the West Florida Escarpment, Gulf of Mexico, is greatly extended to the Barbados accretionary prism in the tropical western Atlantic and to the newly discovered seeps on the west equatorial African margin (Sibuet et al. 2002). In addition to these eight named species, five indeterminate or unnamed species of Alvinocaris have been reported, and most of them are under study by other authors. A new monotypic genus, Shinkaicaris, is established for Alvinocaris leurokolos Kikuchi and Hashimoto, 2000. The new genus is rather closer to Chorocaris Martin and Hessler, 1990, Opaepele Williams and Dobbs, 1995, and Rimicaris Williams and Rona, 1986 than to Alvinocaris in the structure of the eyes and the armament of the telson and percopods. A key to aid in the identification of the eight species of *Alvinocaris* is given, although it is applicable only to adult specimens. The biogeography of Alvinocaris species is discussed.

Keywords: Alvinocarididae, Alvinocaris, Caridea, Crustacea, Decapoda, key to species, new genus, new species, Shinkaicaris

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## Introduction

The caridean genus Alvinocaris was established for A. lusca Williams and Chace, 1982, the first shrimp species discovered and described from hydrothermally influenced fields on the Galapagos Rift, in the eastern Pacific. Since the discovery of A. lusca, seven species assigned to this genus have been described in various reducing environments; two from the Mid-Atlantic Ridge (A. markensis Williams, 1988 and A. williamsi Shank and Martin, 2003), two from Gulf of Mexico cold seeps (A. muricola Williams, 1988 and A. stactophila Williams, 1988) and three from the back-arc basin Okinawa Trough, Ryukyu Islands, Japan (A. longirostris Kikuchi and Ohta, 1995, A. brevitelsonis Kikuchi and Hashimoto, 2000, and A. leurokolos Kikuchi and Hashimoto, 2000). Alvinocaris longirostris is known also from cold seeps at Off Hatsushima site in Sagami Bay, central Japan (Fujikura et al. 1995, 1996). In addition to these species, five indeterminate species are known worldwide. Shank et al. (1999) mentioned the existence of an undescribed species from the Edison Seamount, Bismarck Sea, western Pacific, at a depth of 1483 m. This species is now under study by K. Baba and M. Türkay (personal communication). Two indeterminate species were discovered from the Bay of Plenty, New Zealand (W. R. Webber and J. C. Yaldwyn, personal communication). Recently, Van Dover et al. (2003) reported the occurrence of an indeterminate species from cold seeps on the Blake Ridge, north-western Atlantic. Escobar-Briones and Villalobos-Hiriart (2003) recorded an indeterminate species from Banco Chinchorro in the northern Caribbean at depths of 176–203 m.

The familial assignment of *Alvinocaris* and other shrimp genera associated with vent and seep environments, i.e. *Rimicaris* Williams and Rona, 1986, *Chorocaris* Martin and Hessler, 1990, *Opaepele* Williams and Dobbs, 1995, and *Mirocaris* Vereshchaka, 1997, has been controversial (Williams and Chace 1982; Williams and Rona 1986; Christoffersen 1986; Williams 1988; Martin and Hessler 1990; Segonzac et al. 1993; Williams and Dobbs 1995; Vereshchaka 1997; Shank et al. 1999). However, Komai and Segonzac (2003) have assigned all these genera to the family Alvinocarididae Christoffersen, 1986, showing many possible synapomorphies for this taxon.

This study was initiated to identify material collected from various localities in the Atlantic Ocean, including samples from a newly discovered cold seep area along the west equatorial African margin, located near the Zaïre river canyon, a giant pockmark named Régab, with the Remotely Operated Vehicle (ROV) Victor 6000, during four French cruises (Zaïrov, Biozaïre 1 and 2, and Bioz-Recup Cruises). A recent collection from the German Cruise M56 (RV Meteor) at the Congo Fan, about 100 km north of Régab site, was also included in this study. In attempting to identify this material from the existing literature, it quickly became apparent that some previously described species were not well diagnosed. Also, characters used by previous authors in discriminating species (e.g. shape and length of the rostrum and spination of the percopods) were unreliable or should be treated carefully because of overlap in the range of variation between species. In particular, the original descriptions of two species described by Williams (1988), A. markensis and A. muricola, were based on immature type specimens, and thus, the real diagnostic features of those species have remained unclear. In subsequent descriptions of new species (Kikuchi and Ohta 1995; Kikuchi and Hashimoto 2000; Shank and Martin 2003), the authors compared their material only with these type descriptions. Species of Alvinocaris, as well as other alvinocaridid species, have been the subject of several biological studies (e.g. Hessler and Smithey 1983; Van Dover et al. 1985; Van Dover 1986; Segonzac et al. 1993; Casanova et al. 1993; Vereshchaka 1996; Pond et al. 1997; Wharton et al. 1997; Gaten et al. 1998; Dixon et al. 1999; Gebruk et al. 2000b; Nègre-Sadargues et al. 2000; Kim and Ohta 2001),

and therefore, clarification of their taxonomy became necessary. For this reason, we decided to re-diagnose all previously described species by morphological comparison using the type material and/or supplementary samples from topotypic localities. A monotypic genus, Shinkaicaris gen. nov., is established for Alvinocaris leurokolos. Comparison shows that the species is more closely related to Chorocaris, Opaepele, and Rimicaris than to Alvinocaris. Re-examination of the holotype (male) and allotype (female) of A. stactophila has shown that two species are represented in the type series of this taxon. The specific status of the allotype remains unclear, as only a single immature specimen has been available for study. Four species were confounded in the specimens referred to A. brevitelsonis by Kikuchi and Hashimoto (2000). The true Alvinocaris brevitelsonis is represented only by the holotype; the paratypes and non-paratypes are a mixture of A. dissimilis sp. nov., Opaepele sp. and Shinkaicaris leurokolos. Careful comparison between topotypic adult specimens of A. muricola from cold seeps on the Florida Escarpment and abundant specimens from African margin seeps has shown that there are no morphological differences between the two populations. Therefore, we refer the latter population from the west equatorial African margin to A. muricola, although the two localities are far apart. The occurrence of A. muricola on the Barbados accretionary prism in the tropical western Atlantic is also confirmed. As a result, eight named species of Alvinocaris, including one new species, are recognized in this study. Notes on ecology are given when information is available. Further, biogeography of species of Alvinocaris is briefly discussed.

Four of the five indeterminate species mentioned above are under study by other authors, and therefore these species are only briefly mentioned in this study. The status of the indeterminate species from apparently non-chemosynthetic locations on Banco Chinchorro (Escobar-Briones and Villalobos-Hiriart 2003) remains unknown, because the authors did not provide data on the morphology of their specimens and because no voucher specimens have been available for study. This taxon is not considered in this study.

#### Material and methods

The type material was obtained on loan. Newly obtained collections studied here came from several diving cruises organized by French, American, Portuguese and German teams: Hydrosnake, DS Nautile/RV Atalante, June 1988 (Chief scientist C. Mével), Mid-Atlantic Ridge (MAR), Snake Pit (3500 m); Diapisub, DS Nautile/RV Atalante, December 1992 (Chief scientist B. Mercier de Lépinay), south Barbados, Orénoque A (1700 m); MAR 93, DS Alvin/RV Atlantis and Jean Charcot, June 1993 (Chief scientists C. L. Van Dover and A. Fiala), Snake Pit; Microsmoke, DS Nautile/RV Atalante, November 1995 (Chief scientist D. Prieur), Snake Pit; Diva 1, DS Nautile/RV Atalante, May 1994 (Chief scientist Y. Fouquet), MAR, Menez Gwen (865 m); Diva 2, DS Nautile/RV Atalante, June 1994 (Chief scientist D. Desbruyères), MAR, Menez Gwen; Saldanha, DS Nautile/RV Atalante, July 1997 (Chief scientist F. Barriga), MAR, Menez Gwen; Atos, ROV Victor/RV Atalante, July 2001 (Chief scientist P.-M. Sarradin), MAR, Lucky Strike (1700 m) and Rainbow (2300 m); Zaïrov, ROV Victor/RV Atalante, December 2000 (Chief scientist H. Ondréas), west African margin, Régab (3150 m); Biozäire 1 and 2, ROV Victor/RV Atalante, January and November 2001 (Chief scientist M. Sibuet), west African margin, Régab; Seahma 1, ROV Victor/RV Atalante, August 2002 (Chief scientist F. Barriga), Rainbow; Bioz-Recup, RV Suroît, 20 January to 6 February 2003 (Chief scientist P. Crassous), west African margin, 2 km of Régab; M 56 Cruise, RV Meteor, 10-21 December 2002 (Chief scientist V. Spiess), Congo Fan, ca 100 km north of Régab.

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The material examined is deposited in the collections in the following institutions: Institut français de recherche pour l'exploitation de la mer (Ifremer, Département Environnement profond); Japan Marine Science and Technology Center, Yokosuka (JAMSTEC); Muséum national d'Histoire naturelle, Paris (MNHN, with a code of Na); Natural History Museum, London (NHM); Natural History Museum and Institute, Chiba (CBM, with a code of ZC); National Museum of Natural History, Smithsonian Institution (USNM); and National Science Museum, Tokyo (NSMT, with a code of Cr).

In the systematic account, species are arranged chronologically by the date of the original description. The measurements used for different structures are defined in Figure 1, and should be taken to the nearest 0.1 mm. An indication of specimen size is provided by the postorbital carapace length (CL). Maximal total length, measured from the level of the anterior margin of the antennal scale to the posterior margin of the telson, is also provided for each species.

Common features of the species of *Alvinocaris* are described under the section "General description of adult" accompanied by illustrations of representative parts of *A. muricola*. Differences between species are often so slight that descriptions of each are generally confined to variations in characters from the general description. However, a full description is given for *Shinkaicaris leurokolos* comb. nov., as the species is a sole representative of the proposed new genus.

Descriptive terminology for the mouthparts follows that of Komai and Segonzac (2003), in which confusion regarding the interpretation on the homology of various structures of these appendages in previous literature (e.g. Williams and Chace 1982; Williams 1988; Kikuchi and Ohta 1995; Vereshchaka 1997; Kikuchi and Hashimoto 2000) was substantially clarified.

#### **Systematics**

#### Family ALVINOCARIDIDAE

#### Genus Alvinocaris Williams and Chace, 1982

Alvinocaris Williams and Chace 1982, p 137; Williams 1988, p 263; Kikuchi and Ohta 1995, p 771.

Type species. Alvinocaris lusca Williams and Chace, 1982.

#### Emended diagnosis

Rostrum more than 0.20 of carapace length, always with series of dorsal teeth extending to anterior part of carapace. Carapace with conspicuous, rather high postrostral ridge extending beyond midlength of carapace; branchial region not extremely inflated laterally; antennal and pterygostomian teeth well developed, sharp; inferior orbital angle not delineated; lateral surface with shallow post-antennal groove extending from base of antennal tooth and slightly to strongly diverging from anterior to posterior with horizontal plane of dorsal margin of carapace continuous with rudimentary hepatic groove. Fourth and fifth abdominal pleura usually dentate posterolaterally. Telson with dorsolateral spines arranged in straight rows; posterior margin rounded, with row of flexible, plumose setae and/or rigid spines. Eyes narrowly fused mesially with indication of median separation,



Figure 1. Diagrammatic *Alvinocaris*, showing measurements used in text. (A) Carapace and rostrum, lateral; CL, carapace length; DA, dorsal angle; RL, rostral length. (B) Carapace, dorsal: CW, carapace width. (C) Anterior part of carapace and cephalic appendages, dorsal; L, length; W, width. (D) Sixth abdominal somite, lateral; L, length; H, height. (E) Telson, dorsal; AW, anterior width; L, length; PW, posterior width. (F) Antennal scale, dorsal; abbreviations as in (C). (G) Chela of first pereopod, lateral; PL, palm length; PH, palm height.

lacking corneal facets, but usually with diffused pigmentation inside; anterior surface dorsally with small acute or subacute tubercle. Antennal scale oval, not locked with antennule, with sharp distolateral tooth. Third maxilliped to fourth pereopods without strap-like epipods. Ischium of second pereopod with one spine ventrolaterally. Dactyli of third to fifth pereopods compressed laterally, each with single row of accessory spinules on ventral margin; meri of third and fourth pereopods with one to four spines on ventrolateral surface; ischia of third and fourth pereopods each with one or two spines ventrolaterally. Second to fourth pleopods each with slender, simple appendix interna in both sexes; fifth pleopod with well-developed appendix interna bearing terminal cluster of cincinnuli.

## General description of adult

Integument of body thin, but not membranous, surface shining.

Rostrum compressed laterally, sharply pointed, length and curvature variable intra- or interspecifically; dorsal margin always armed with series of fixed teeth diminishing in size anteriorly and usually extending to anterior part of carapace; lateral carina conspicuous, broadened proximally and confluent with orbital margin; ventral margin usually armed with small fixed teeth. Carapace somewhat compressed laterally; postrostral ridge rather high, extending beyond midlength of carapace; antennal and pterygostomian teeth sharp; inferior orbital angle not delineated; lateral surface with shallow post-antennal groove passing obliquely ventrally and extending to hepatic region. Strong median sternal spine between coxae of fifth pereopods.

Abdomen smooth dorsally; pleural margin of anterior two somites broadly rounded, that of third somite rounded or obscurely serrate or dentate, those of fourth and fifth somites usually each with at least posterolateral tooth. Sixth somite with sharp posterolateral process and posteroventral tooth. Telson elongate subrectangular, with straight row of six to nine dorsolateral spines on either side; posterior margin usually rounded, with row of more than 10 plumose setae or spines.

Eyes on basally movable stalks narrowly fused mesially (cf. Figure 4B); division of corneal region and stalk unclear; corneal region, shrunken, unfaceted, with irregular, scattered pigment-like masses within stalk; dorsal surface of corneal region slightly folded, anterodorsal surface flattened or slightly concave, margins of that surface and dorsal fold converging in small anterior spiniform tubercle.

Antennular peduncle moderately stout to stout. First segment with conspicuous fossa on dorsal surface subproximally, and with conspicuous distolateral spine; stylocerite slender, reaching or overreaching distal margin of second peduncular segment, slightly depressed dorsoventrally, sharp, separated from first segment by narrow, deep incision and succeeding deep groove; dorsal surface of stylocerite with distinct rounded tubercle subproximally and transverse row of setae somewhat distal to subproximal tubercle. Second segment with distomesial spine. Third segment short. Dorsolateral flagellum longer than carapace, thickened aesthetasc-bearing portion in basal 0.40–0.50; ventromesial flagellum somewhat longer than dorsolateral flagellum.

Antenna with stout basicerite bearing ventrolateral distal spine and ventral submarginal spine. Antennal scale broad, with sharp distolateral tooth. Carpocerite stout. Antennal flagellum much longer than body, with many, close-set annulations.

Mandible (Figure 2B) with distinct separation of incisor process and molar process; incisor process broad, armed with row of teeth on mesial margin, dorsal (inner) surface concave; molar process simple, its narrowly rounded tip minutely setose; palp



Figure 2. *Alvinocaris muricola* Williams, 1988. Left appendages. (A) Antennal scale, dorsal; (B) mandible, dorsal; (C) maxillule, ventral; (D) maxilla, ventral; (E) first maxilliped, ventral; (F) endopod of first maxilliped, dorsal; (G) second maxilliped, ventral; (H) first pleopod, ventrolateral; (I) endopod of first pleopod; (J) appendices interna and masculina of second pleopod, mesial. (A–H) Female from Régab site, west equatorial African margin (CL 16.8 mm; MNHN-Na 14277); (I, J) male from same locality (CL 15.4 mm; Ifremer).

two-articulated, basal article longer than distal article, somewhat curved mesially; distal article broadly spatulate, with numerous short to long setae marginally. Maxillule (Figure 2C) with coxal endite asymmetrically oval-triangular, with numerous short setae on mesial to anterior margin; basial endite with narrowed base but broadened distally, armed with numerous short spines arranged in two rows and with mesial spines partially obscured by submarginal row of setae; palp scarcely bifurcated, with long spiniform seta on obsolescent proximomesial lobe, and two or three much shorter adjacent submarginal setae on distal lobe. Maxilla (Figure 2D) with subtriangular coxal endite represented by single lobe; basial endite bilobed, proximal lobe subrectangular, distal lobe subtriangular, both with dense marginal and submarginal setae; palp narrow, somewhat twisted; scaphognathite with anterior lobe broad, rectangulo-ovate, fringed with long setae on anterior and mesial margins, shorter setae along entire lateral margin, posterior lobe narrow and somewhat elongate, fringed on blunt tip and adjacent mesial margin by strikingly long setae preceded proximally by shorter setae similar to those on lateral margin. First maxilliped (Figure 2E) with small, mesially setose coxal endite; basial endite irregularly fusiform, strongly convex on ventral (outer) surface and deeply concave on dorsal (inner) surface, with numerous submarginal, dorsally curved setae on ventral surface; endopod (Figure 2F) concealed by exopod, short, rather abruptly narrowed at about distal 0.30; exopod greatly expanded, leaf-like, fringed marginally by long plumose setae, flagellum completely reduced; epipod large, obscurely bilobed. Second maxilliped (Figure 2G) with endopod six-segmented, somewhat pediform but flattened; coxa and basis-ischium fused segment with row of dorsally curved, fine long setae on mesial margin; merus much shorter than basis-ischium fused segment; carpus very short; propodus narrow, lacking row of spines on mesial margin, but with setae; dactylus tapering terminally, articulating with distal part of propodus, with dense setae on mesial face and blunt tip; exopod absent; epipod subovate or subrectangular, with slender, non-lamellate podobranch directed forward. Third maxilliped (Figure 3A, B) slender, composed of four segments, reaching slightly beyond distal end of antennal scale; distal two segments slightly arched in lateral view; ultimate segment trigonal in cross-section, tapered distally, bearing two or three small terminal spines, row of short setae on dorsal and ventral margins, and transverse tracts of dense setae along mesial face; carpus (penultimate segment) shorter than ultimate segment, also with transverse tracts of setae on mesial face; antepenultimate segment (fused merus-ischium-basis) subequal to distal two segments combined, somewhat sinuously curved in dorsal view, distal half weakly compressed laterally and proximal half somewhat flattened dorsoventrally, with slender, curved spine at distolateral ventral corner, margins with short to long setae; tufts of long setae at proximomesial portion of antepenultimate segment; coxa with small rounded process bearing terminal setae and feebly bifurcated epipod; exopod absent.

First pereopod (Figure 3C) reaching about as far as third maxilliped, moderately to fairly robust, exhibiting polymorphism apparently correlated to growth. Fingers curved downward and inward; length of dactylus quite variable; outer surface of both fingers convex, inner concavity with opposed edges uniformly offset, closing without gape, each armed with fine row of almost uniform erect corneous teeth so closely set as to be contiguous, tip of each finger slightly spooned; row of tufts of short sensory setae on inner surface submarginally along cutting edges. Palm extremely short to moderately long (showing tendency to become proportionally longer and stouter with increase of size), weakly to somewhat inflated. Carpus cupped distally to receive palm; dorsodistal margin with blunt to subacute projection mesially; ventral surface flared into strong lateral ridge terminating in small to large tooth and smaller mesial ridge ending in smaller blunt tooth, surface



Figure 3. *Alvinocaris muricola* Williams, 1988. Left thoracic appendages. (A) Third maxilliped, lateral; (B) coxa and antepenultimate segment of third maxilliped, dorsal; (C) first pereopod, lateral; (D) carpus of first pereopod, mesial; (E) second pereopod, lateral; (F) chela of second pereopod, dorsal; (G) third pereopod, lateral; (H) dactylus of third pereopod, lateral; (I) fourth pereopod, lateral; (J) fifth pereopod, lateral; (K) dactylus of fifth pereopod, lateral. Female from Régab site, west equatorial African margin (CL 16.8 mm; MNHN-Na 14277).

between ridges with dense grooming setae and one to three small movable spines (Figure 3D); mesial face with shallow depression. Merus and ischium strongly obliquely articulated in lateral view; merus sometimes inflated ventrally, occasionally with small subdistal tooth on ventrolateral margin; ischium always unarmed.

Second percopod (Figure 3E) shorter and more slender than first percopod, not reaching distal margin of antennal scale. Fingers 0.90–1.10 times as long as palm, each terminating in small corneous unguis crossing each other when closed, cutting edges without gape, each pectinate with single row of minute teeth directed obliquely distally and increasing slightly in size (Figure 3F). Carpus slightly longer than chela. Merus and ischium obliquely articulated in lateral view. Ischium with one ventrolateral spine.

Third to fifth percopods (Figure 3G, I, J) moderately long for family, generally similar in length and structure, third reaching beyond distal margin of antennal scale by 0.40–0.70 length of propodus. Propodus–carpus combined shorter than merus–ischium combined in third, subequal in fourth, and longer in fifth. Dactyli (Figure 3H, K) short (0.08–0.15 of propodus length), armed with four to six corneous spines on flexor margin grading from small proximally to longest and strongest distally. Propodi of third and fourth percopods with slender spinules arranged in two rows on ventral surface; propodus of fifth percopod with numerous spiniform setulose setae arranged in three or four rows on distal half of ventral surface. Carpi distinctly shorter than propodus, with dorsodistal process. Meri each with one to four movable spines ventrolaterally in third and fourth, zero to two spines in fifth. Ischia usually each with two (rarely one) ventrolateral spines in third and fourth percopods, zero to two (usually one) spine in fifth.

First to fourth percopods each with small pre-coxal spine visible in posterolateral view.

Branchial formula summarized in Table I. Pleurobranchs on fourth to eighth thoracic somites becoming progressively larger posteriorly. Arthrobranchs on third to seventh thoracic somites more nearly uniform in size (that on seventh somite slightly smaller than others). Epipods and exopods absent on percopods.

Pleopods well developed. First pleopod (Figure 2H) with endopod 0.50–0.60 length of exopod, sexually dimorphic; in males (Figure 2I), distal part of endopod feebly bilobed, bearing four to six long spiniform setae; in females (Figure 2H), distal part bluntly pointed, with fringe of plumose setae similar to those fringing remaining margins. Second to fifth pleopods with endopods developed as in Figure 1H, slightly

Thoracic somite	1	2	3	4	5	6	7	8
	Maxillipeds			Pereopods				
Appendages	1	2	3	1	2	3	4	5
Pleurobranchs	_	_	_	+	+	+	+	+
Arthrobranchs	_	_	_	1	1	1	1	_
Podobranchs	_	r	_	_	_	-	-	-
Epipods	+	+	+	_	_	_	_	_
Exopods	$+^{a}$	_	_	_	_	_	_	_
Setobranchs	-	-	-	-	-	-	-	-

Table I. Branchial formula of the genus Alvinocaris.

r, rudimentary.

<sup>a</sup>Flagellum absent.

shorter than exopods; appendices internae on second to fourth pleopods not greatly reduced in size, but slender, that on second pleopod (cf. Figure 2J) simple, without terminal cluster of cincinnuli, but those on third and fourth pleopods with few cincinnuli; appendix interna on fifth pleopod more stout than others, with terminal cluster of cincinnuli. Appendix masculina (Figure 2J) moderately robust for family, slightly shorter than appendix interna, with several (up to 12) long, terminal and subterminal bristles.

Uropod with rami subequal in length, exopod with small movable spine mesial to smaller distolateral tooth and sinuous diaeresis.

#### Composition (named species only)

Alvinocaris lusca Williams and Chace, 1982 (type species of the genus); A. markensis Williams, 1988; A. muricola Williams, 1988; A. stactophila Williams, 1988; A. longirostris Kikuchi and Ohta, 1985; A. brevitelsonis Kikuchi and Hashimoto, 2000; A. williamsi Shank and Martin, 2003; A. dissimilis sp. nov.

#### Remarks

The genus *Alvinocaris* is distinguished from other alvinocaridid genera by the presence of a relatively well-developed postrostral ridge extending beyond the midlength of the carapace, the possession of a small spiniform tubercle on the anterior surface of the eye, the narrowly fused eyes and the presence of meral spines on the third and fourth percopods. In the other alvinocaridid genera (Chorocaris, Mirocaris, Opaepele, Rimicaris, and Shinkaicaris gen. nov.), the postrostral ridge is absent, or if present, does not reach the midlength of the carapace, the eyes are broadly fused mesially without trace of a median separation, and the meri of the third and fourth percopods are devoid of ventrolateral spines. Furthermore, the styliform, dorsally dentate rostrum separates Alvinocaris and Shinkaicaris from Chorocaris, Mirocaris, Opaepele, and Rimicaris. In the latter four genera, the rostrum is flattened dorsoventrally, and its dorsal surface is slightly carinate and minutely dentate (Opaepele) or rounded (Chorocaris, Mirocaris, and Rimicaris). The dorsolateral spines on the telson arranged in a straight row, and the possession of a single row of accessory spines on the ventral margins of the dactyli of the third to fifth percopods, distinguish Alvinocaris from Chorocaris, Opaepele, Rimicaris, and Shinkaicaris gen. nov. In the latter genera, the dorsolateral spines on the telson are arranged in a sinuous row, and the accessory spines on the dactyli of the third to fourth percopods are arranged in three or four rows on the ventral surfaces. However, most of these features characterizing Alvinocaris appear plesiomorphic, as they are shared with the genus Bresilia Calman, 1896, the sister group of the Alvinocarididae (Christoffersen 1986; Komai and Segonzac 2003). Nevertheless, the monophyly of *Alvinocaris* may be suggested by the possession of a small tubercle on the anterodorsal surface of the eye, as this feature is not known in other alvinocaridid or bresilioid taxa.

As the above comparison suggests, *Alvinocaris* appears the most basal assemblage within the Alvinocarididae. Further, the structure of the eye-stalks of *Alvinocaris* is intermediate between the well-developed, clearly separated eyes shown by most carideans and the broadly fused condition exhibited by other alvinocaridid genera. However, Shank et al. (1999) hypothesized that *Mirocaris* and the other alvinocaridid genera (as Bresiliidae) are sister groups. A phylogeny of the alvinocaridid shrimps based on morphological data will be discussed in a separate paper.

In *Alvinocaris*, size-related morphological variation is seen in the length of the rostrum, dorsal angle of the carapace, position of the posteriormost tooth of the dorsal rostral series, width of the telson, width of the antennal scale, shape of the chela of the first pereopod, and stoutness of the third to fifth pereopod. With increasing size, the length of the rostrum reduces, the dorsal angle of the carapace becomes sharper, the dorsal series of teeth extends more posteriorly, the width of the telson and antennal scale become great. Further, the shape of the chela of the first pereopod is variable with increasing size, as the palm is lengthened and thickened, and the dactylus becomes proportionally shorter. The third to fifth pereopods become stouter with increase of body size. The terminal conditions of these characters provide diagnostic features for species discrimination (see below). Note, however, that most of these features are not differentiated in juvenile or subadult specimens, and therefore, morphology-based identification of juvenile or subadult specimens is sometimes extremely difficult.

The armature of the third to fifth abdominal pleura is also highly variable in most species. No apparent correlation with sex or size is recognized in this variation. Certain degree of abnormality is seen in the shape and armature of the rostrum (e.g. *A. muricola*). This abnormality of the rostrum may be caused by injury and regeneration.

Species of the genus are generally very similar to one another. Williams (1988) suggested some minor differences that may provide specific significance for discrimination of Alvinocaris species. These include features such as the number of incisor teeth on the mandible, number of spines on the maxillule, shape of the maxilla, number of meral spines on the fifth percopod, distribution of spines on the ischia of the third to fifth percopods, and the shape of the endopod of the male first pleopod and appendix masculina. However, we have found most of these features to be unreliable because of interspecific overlap, particularly the shape of the maxilla and the shape of the pleopodal structure that were found to be largely affected by change in size. The number of pereopod meral spines is variable and overlaps among species. Further, in his original descriptions of A. markensis, A. muricola, and A. stactophila, Williams (1988) described the ischium of the second percopod as unarmed in these three species. However, our re-examination of the type material of these species has shown that there is one movable spine on the ventrolateral face of the ischium of the second percopod in all three species. Although the armature of the ischium of the second percopod has been used as one of the diagnostic characters in distinguishing species of Alvinocaris (Kikuchi and Ohta 1995; Kikuchi and Hashimoto 2000), the presence of this spine is stable within *Alvinocaris*.

During this study, the following characters were found to be useful in discriminating species of *Alvinocaris*: the length of the rostrum, the number of dorsal and ventral teeth on the rostrum, the position of the posteriormost tooth of the rostral series, the degree of inflation of the branchiostegal region of the carapace, the degree of the projection of the pterygostomian tooth, armature of the fourth abdominal pleuron, shape of the sixth abdominal somite (represented by the ratio "length/proximal height"), shape of the telson, armature of the posterior margin of the telson, stoutness of the antennular peduncle (represented by the ratio "length/width" of the penultimate segment), shape of the antennal scale (represented by the ratio "length/width"), direction of the distolateral tooth of the antennal scale, shape of the chela of the first percopod; and stoutness of the merus of the third percopod. However, many of these features should be used with caution, as they exhibit large size-related variations, as mentioned above. Particularly, large variation in the length

and armature of the rostrum is observed in A. muricola sp. nov., which diminishes the usefulness of the rostral character for species discrimination.

The following key should be used with caution, as it is designed solely for identifying adult specimens. For identification of juvenile and subadult specimens, the locality records will be helpful, as most species are geographically or bathymetrically separated.

#### Key to named species of Alvinocaris (adults)

1. _	Posterior margin of telson with more than two pairs of spines2Posterior margin of telson with two pairs of spines at lateral corners and 10–16plumose setae4
2.	Ventral margin of rostrum with one tiny tooth; posterior margin of telson with mesial spines of subequal length, lacking plumose setae mesially . <i>A. stactophila</i> [central Gulf of Mexico, 534 m]
_	Ventral margin of rostrum with two or more teeth; posterior margin of telson with mesial spines of greatly unequal length and one to three mesial pairs of short plumose setae
3.	Rostrum with less than five ventral teeth; antennal scale more than 2.2 times longer than wide
-	Rostrum with more than five ventral teeth; antennal scale about 1.9 times longer than wide.
4.	Rostrum usually unarmed on ventral margin; second segment of antennular peduncle about 1.1–1.2 times as long as wide; antennal scale about 0.4 times as long as carapace; telson broad, length 2.2–2.5 times of anterior width.
_	[Menez Gwen, Mid-Atlantic Ridge, 850 m] Rostrum usually armed with teeth on ventral margin; second segment of antennular peduncle more than 1.3 times as long as wide; antennal scale about half length of carapace; telson narrow, length 2.1–3.2 times of anterior width 5
5.	Rostrum with less than three ventral teeth; pterygostomian tooth not strongly produced anteriorly; penultimate segment of antennular peduncle 1.4–1.5 times longer than wide
_	Rostrum usually with more than three ventral teeth; pterygostomian tooth of carapace strongly produced anteriorly; second segment of antennular peduncle more than 1.8 times longer than wide; distolateral tooth of antennal scale usually with straight mesial margin
6.	Anterior part of branchial region somewhat inflated, strongly convex [carapace width 0.7–0.8 of carapace length; rostrum not reaching distal margin of third segment of antennular peduncle in females, occasionally overreaching it in males; posteriormost 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

 [Florida Escarpment, Gulf of Mexico, 3277 m; Barbados accretionary prism, 1697 m; west equatorial African margin, off Congo, 3113–3150 m]
Anterior part of branchial region not particularly inflated, only slightly convex

- Rostrum usually not reaching distal margin of antennular peduncle in both males and females; posteriormost tooth of dorsal rostral series arising from 0.24–0.31 of carapace length; second segment of antennular peduncle 1.8–2.0 times longer than wide; antennal scale 1.9–2.1 times longer than wide . . . A. markensis [Lucky Strike to Logatchev, Mid-Atlantic Ridge, 1693–3650 m]

Alvinocaris lusca Williams and Chace, 1982 (Figures 4, 5, 29)

- Alvinocaris lusca Williams and Chace 1982, p 137, Figures 1–7 [type locality: Rose Garden area, Galapagos Rift, 00°48.15'N, 86°13.29'W, 2450 m]; Shank 1997, p 191; Shank et al. 1999, p 246 (Table 1), Figure 2.
- Not Alvinocaris lusca: Fustec et al. 1987, p 129.=Lebbeus carinatus de Saint Laurent, 1984 (not Lebbeus carinatus Zarenkov, 1976).

#### Material examined

Galapagos Rift. DS *Alvin*: dive 990, Rose Garden area, 00°48.15′N, 86°13.29′W, 2450 m, 9 December 1979, one male CL 7.2 mm, 10 females CL 7.1–13.5 mm (paratypes; USNM 184537).

#### Description

Body moderately robust.

Rostrum (Figure 4C) slightly descending or directed forward, straight, 0.37-0.44 times carapace length, usually reaching second segment of antennular peduncle, but rarely not exceeding first segment; dorsal margin with slightly convex or straight general outline, armed with 10–14 teeth including four to six moderately large teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.32-0.39 of carapace length; ventral margin armed with three or four small teeth on anterior 0.20-0.40. Carapace (Figure 4A–D) width 0.55-0.67 of length; postrostral median ridge relatively low, extending to 0.60-0.70 of carapace length, dorsal angle about  $170^\circ$ ; pterygostomian tooth weakly produced anteriorly, smaller than antennal tooth, at most only slightly reaching beyond antennal tooth; post-antennal groove very shallow; branchial region not particularly inflated.

Third abdominal pleuron unarmed marginally. Fourth abdominal pleuron (Figure 4E) with one to five (most frequently four) posterolateral teeth. Fifth abdominal pleuron similarly armed with strong posteroventral tooth and additional one to five small teeth. Sixth somite 1.50–1.70 times longer than height. Telson (Figure 5A) not reaching to



Figure 4. *Alvinocaris lusca* Williams and Chace, 1982. (A) Carapace and cephalic appendages, lateral (rostrum broken off); (B) anterior part of carapace and cephalic appendages, dorsal; (C) same, lateral; (D) carapace, dorsal (rostrum broken off); (E) third to sixth abdominal somites, lateral. (A, B, D, E) Paratype female from Rose Garden area, Galapagos Rift (CL 13.5 mm; USNM 184537); (C) paratype female (CL 8.6 mm; same lot).



Figure 5. *Alvinocaris lusca* Williams and Chace, 1982. (A) Telson and right uropod, dorsal; (B, C) posterior part of telson, dorsal; (D) right antennal scale, dorsal (marginal setae omitted); (E) first pereopod, lateral; (F) chela of first pereopod, outer; (G) left third pereopod, lateral; (H) dactylus and distal part of propodus of left third pereopod, lateral. (A, B, D–H) Paratype female from Rose Garden area, Galapagos Rift (CL 13.5 mm; USNM 184537); (C) paratype (CL 8.6 mm; same lot).

slightly overreaching posterior margin of uropodal endopod, very slightly narrowed posteriorly, length 3.20–3.30 times anterior width and 4.10–4.30 times posterior width; armed with seven to nine dorsolateral spines; posterior margin (Figure 5B, C) shallowly notched medially or slightly convex, armed with six to nine pairs of spines (mesial four to seven spines unequal in length) and one or two short plumose setae on either side of median notch.

Antennular peduncle (Figure 4B) moderately stout, second segment 2.00–2.20 times longer than wide. Antennal scale (Figure 5D) about half length of carapace, 2.20–2.60 times longer than wide; lateral margin slightly convex to straight, subparallel with dorsal median ridge; distolateral tooth relatively narrow, directed forward, not reaching distal margin of somewhat produced, rounded blade.

First percopod as illustrated (Figure 5E); palm (Figure 5F) at most 1.26 times longer than height; dactylus longer than palm. Third percopod (Figure 5G) relatively slender for genus; dactylus (Figure 5H) with accessory spinules notably increasing in size distally; carpus 0.70–0.75 times as long as propodus; merus about 8.00 times as long as greatest height.

#### Size

Largest male 7.3 mm; largest female 13.5 mm, ovigerous females unavailable. Maximal TL ca 85 mm.

#### Variation

As is apparent from the above description, the shape of the posterior margin of the telson is variable from shallowly notched medially to weakly convex.

#### Distribution and habitat

Known with certainty only from the Galapagos Rift, Rose Garden area, 00°N, 2450 m, and East Pacific Rise, 9°N, 2520 m (Figure 29) (Williams and Chace 1982; Shank et al. 1999).

This species is associated with the vestimentiferan worm *Riftia pachyptila* Jones, 1980, and could be nourished from its biological production, as Hessler and Smithey (1983) briefly reported ecology and behaviour of this species at the Rose Garden site. Van Dover et al. (1985) described planktotrophic larval development of this species.

#### Remarks

During this study, 11 paratypic specimens have been examined. They are generally consistent with the original description provided by Williams and Chace (1982), although the shape of the posterior margin of the telson was found to be variable (see "Variation").

The possession of more than two pairs of spines on the posterior margin of the telson is shared by *A. lusca*, *A. stactophila*, and *A. brevitelsonis*. The narrow antennal scale distinguishes *A. lusca* from other congeneric species, not only from *A. stactophila* and *A. brevitelsonis* (the antennal scale is 2.20–2.60 times as long as wide in *A. lusca*, less than 2.10 times as long in other species). *Alvinocaris stactophila* is immediately distinguished from *A. lusca* and *A. brevitelsonis* by the possession of only one tooth on the ventral margin of the rostrum, and the size and composition of the armature on the posterior margin

of the telson. In *A. lusca* and *A. brevitelsonis*, there are three to six (in *A. lusca*) or seven (*A. brevitelsonis*) ventral teeth on the rostrum (Williams and Chace 1982; present study). The armature of the posterior margin of the telson (except for the two lateral pairs of spines) consists only of spines in *A. stactophila*, while in *A. lusca* and *A. brevitelsonis*, it contains four to five pairs of spines and one or two pairs of short plumose setae. The spines on the posterior margin of the telson are subequal in length in *A. stactophila*, but they are distinctly unequal in *A. lusca* and *A. brevitelsonis* (particularly, the spine just mesial to the longer spine of the two lateral spines is much shorter than other spines). The shape and length of the rostrum provide subtle differences among the three species. In *A. lusca*, the rostrum is straight with the dorsal outline occasionally being slightly convex, and does not reach the distal margin of the penultimate segment of the antennular peduncle; it is very slightly curved dorsally and does not reach the distal margin of the second segment of the antennular peduncle in *A. stactophila*; it is somewhat curved dorsally and reaches the distal margin of the second segment of the antennular peduncle in *A. brevitelsonis*.

Fustec et al. (1987) recorded Alvinocaris lusca from a vent site on the East Pacific Rise at 13°N. However, the occurrence of this species at this site is questionable, as there have been no subsequent records of A. lusca from this location in spite of intensive sampling effort. It is possible that Fustec et al. (1987) misidentified Lebbeus carinatus de Saint Laurent, 1984 (the name is a junior homonym of Lebbeus carinatus Zarenkov, 1976, but no replacement name has been proposed), a common shrimp species at this site, as Alvinocaris lusca.

#### Alvinocaris markensis Williams, 1988

(Figures 6, 7, 14A, 29)

*Alvinocaris markensis* Williams 1988, p 264, Figures 1, 2, 7 [MARK vent, Snake Pit, Mid-Atlantic Ridge, 23°22.09'N, 44°57.12'W, 3437 m]; Dixon and Dixon 1996, p 9, Figures 1–3; Vereshchaka 1996, p 577; Shank 1997, p 192; Shank et al. 1998, p 89; Shank et al. 1999, p 246 (Table 1), 247, Figure 2; Kikuchi and Hashimoto 2000, p 146 (table), 148 (key); Desbruyères et al. 2000, p 209 (Table 4).

Alvinocaris muricola: Shank et al. 1999, p 246 (Table 1). Not Alvinocaris muricola Williams, 1988.

Alvinocaris aff. markensis: Desbruyères et al. 2001, p 1335 (Table 3).

#### Material examined

Mid-Atlantic Ridge. DS *Alvin*: dive 1683, stn 1, MARK vent, Snake Pit, 23°22.09'N, 44°57.12'W, 3437 m, 30 May 1986, scoop, one female CL 4.2 mm (holotype; USNM 234286); same data, one female CL 6.7 mm, one juvenile CL 4.4 mm (paratypes; USNM 234287).

Hydrosnake (DS *Nautile*): HS 03, site Elan, Snake Pit, 3515 m, 21 June 1988, 4 males CL 9.5–12.9 mm (MNHN-Na 14279); HS 10, site Les Ruches, Snake Pit, 23°22.13'N, 44°57.13'W, 3482 m, 28 June 1988, slurp gun, one female CL 18.9 mm, one juvenile (badly damaged) (MNHN-Na 15049).

MAR 93 (DS *Alvin*): M11/2619, site Les Ruches, Snake Pit, 23°22.13'N, 44°57.13'W, 3482 m, 20 June 1993, one male CL 6.9 mm, two females CL 6.1, 6.2 mm (MNHN-Na 14280); same data, one female CL 18.3 mm (MNHN-Na 14281).

Microsmoke (DS *Nautile*): dive MS 08, site Les Ruches, Snake Pit, 23°22.13'N, 44°57.13'W, 3480 m, baited trap, 21 November 1995, one male CL 10.2 mm, 13 females



Figure 6. *Alvinocaris markensis* Williams, 1988. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) carapace, dorsal; (D) third to sixth abdominal somite, lateral; (E) telson and right uropod, dorsal; (F) posterior part of telson, dorsal. Female from site Les Ruches, Snake Pit, Mid-Atlantic Ridge (CL 16.7 mm; MNHN-Na 14282).



Figure 7. *Alvinocaris markensis* Williams, 1988. (A) Left antennal scale, dorsal; (B) left first pereopod, lateral; (C) chela of left first pereopod, outer; (D) left third pereopod, lateral; (E) dactylus and distal part of propodus of left third pereopod, lateral. Female from site Les Ruches, Snake Pit, Mid-Atlantic Ridge (CL 16.7 mm; MNHN-Na 14282).

CL 7.3–16.7 mm (MNHN-Na 14282); same dive, two females CL 9.4, 12.8 mm, five specimens (sex undeterminable because of lack of abdomens) CL 10.0–12.0 mm (MNHN-Na 15050); dive MS 16, same site, 3500 m, 29 November 1995, one female CL 22.3 mm (MNHN-Na 14283); same data, four females CL 13.7–18.1 mm (MNHN-Na 15051).

Atos (ROV *Victor*): dive 119-17, Tour Eiffel, Lucky Strike, 37°13.48'N, 32°19.42'W, 1693 m, 16 July 2001: one ovigerous female CL 13.0 mm (MNHN-Na 14284); dive 104-02, 25 June 2001, GBT1, site Rainbow, 36°13.759'N, 33°54.169'W, 2292 m, one male CL 10.1 mm (MNHN-Na 14285); three juveniles, dive 107-05, same site, 30 June 2001, slurp gun, one female CL 8.3 mm, one juvenile CL 4.9 mm (Ifremer).

Seahma 1: dive 186-04, Rainbow, 36°13.759'N, 33°54.169'W, 2292 m, 8 August 2002, slurp gun, one female CL 13.0 mm (CBM-ZC 7041).

#### Description

Body moderately robust.

Rostrum (Figure 6A, B) directed forward or slightly descending, nearly straight or slightly curved dorsally, 0.45–0.70 of carapace length, usually reaching to second segment

of antennular peduncle; dorsal margin nearly straight or slightly concave in general outline, armed with 14–19 teeth, including 8–12 on rostrum proper and five to seven moderately large teeth on carapace posterior to level of orbital margin, posteriormost tooth arising from 0.24–0.31 of carapace length; ventral margin armed with six to nine small teeth on anterior 0.30–0.50. Carapace (Figure 6A, C) 0.52–0.65 times as wide as long; postrostral median ridge relatively high, strongly compressed laterally, extending to 0.75–0.80 of carapace length with dorsal angle  $150^{\circ}$ ; pterygostomian tooth larger than antennal tooth, distinctly exceeding antennal tooth; post-antennal groove shallow; branchial region not particularly inflated.

Third abdominal pleuron smooth or bearing few minute denticles posteriorly. Fourth abdominal pleuron (Figure 6D) with one to four (most frequently two or three) teeth posteriorly. Fifth abdominal pleuron similarly armed with one strong posterolateral tooth and one to three additional teeth on posterior margin. Sixth somite about 1.50–1.70 times longer than proximal height. Telson (Figure 6E) narrowed posteriorly, not reaching or reaching posterior margin of uropodal endopod, length 2.60–2.90 times anterior width and 4.90–5.10 times posterior width; armed with six to eight dorsolateral spines; posterior margin (Figure 6F) always convex, armed with two pairs of lateral spines and 12–14 plumose setae all longer than mesial pair of lateral spines.

Antennular peduncle (Figure 6B) moderately stout, second segment 1.79–2.05 times longer than wide. Antennal scale (Figure 7A) 0.48–0.51 times as long as carapace, 1.91–2.04 longer than wide; lateral margin straight, slightly diverging anteriorly from dorsal median ridge; distolateral tooth directed forward, falling short of distal margin of blade.

First percopod (Figure 7B, C) as illustrated; greatest height of palm about 0.40 times length of chela; dactylus longer than palm (Figure 7C). Third percopod (Figure 7D) moderately slender; dactylus (Figure 7E) with accessory spinules notably increasing in size distally; carpus 0.65–0.70 times as long as propodus; merus about 7.00 times as long as greatest height.

#### Size

Largest male 12.9 mm; largest female 22.3 mm, ovigerous female 13.0 mm. Maximal TL ca 82 mm.

#### Variation

The shape and armature of the rostrum is rather constant in the present material of this species. The armature of the third to fifth abdominal pleura is variable as in *A. longirostris* (cf. Kikuchi and Ohta 1995).

#### Distribution

The occurrence of this species is confirmed at the three locations on the Mid-Atlantic Ridge: Snake Pit, 3484–3515 m; Lucky Strike, 1693 m; and Rainbow, 2292 m (Figure 29). Shank et al. (1999) recorded *A. markensis* from hydrothermal vents of Broken Spur (3300 m), TAG (3650 m) and Logatchev (3010 m).

#### Ecology

Observations made from video films taken by DS *Nautile* during the cruises Hydrosnake and Microsmoke on the site Snake Pit (Les Ruches, 3480 m and Elan, 3515 m), and by the

ROV Victor during the cruises Atos on the site Lucky Strike (Tour Eiffel, 1693 m) and Seahma 1 on the site Rainbow (2292 m), are consistent with the previous report from Snake Pit and Logatchev (Segonzac et al. 1993; Gebruk et al. 2000a, 2000b). This species always lives solitary at the base of the active chimneys or on the walls of the few active chimneys (Figure 14A), close to aggregates of *Rimicaris exoculata* or on mussel beds. The trophic mode is necrophagous, as capture of the shrimps by baited traps indicates. However, the gut contents examined generally contained much mineral particles.

## Remarks

The holotype and two paratypes of *Alvinocaris markensis* are all juveniles. The species is rediagnosed in this study using supplementary adult specimens from some hydrothermally influenced fields on the Mid-Atlantic Ridge, including topotypic specimens (see "Material examined"). The rostrum normally reaching the second segment of the antennular peduncle and the possession of plumose setae on the posterior margin of the telson link *A. markensis* to *A. muricola*, *A. longirostris*, and *A. dissimilis* sp. nov. Differences among these four species are discussed under "Remarks" for *A. dissimilis* sp. nov.

Desbruyères et al. (2001) mentioned the occurrence of A. aff. markensis at Lucky Strike on the Mid-Atlantic Ridge. The presence of A. markensis at this site has been confirmed based on one ovigerous specimen collected during the Atos cruise (MNHN-Na 14284).

#### Alvinocaris muricola Williams, 1988

(Figures 2, 3, 8–14, 29)

Alvinocaris muricola Williams 1988, p 268, Figures 3, 4, 7 [type locality: West Florida Escarpment, Western Atlantic, 26°01'N, 84°54.61'E, 3277 m]; Shank et al. 1999, p 246 (Table 1), Figure 2; Kikuchi and Hashimoto 2000, p 146, 148 (key).

Alvinocaris cf. muricola: Olu et al. 1996, p 371 (Table 3).

## Material examined

Gulf of Mexico. DS *Alvin*: dive 1754, West Florida Escarpment, 26°01'N, 84°54.61'W, 3277 m, 15.10.1986, one male CL 6.4 mm (holotype; USNM 234288); same data, one female CL 6.4 mm (allotype; USNM 234289); dive 3636, Florida Escarpment, 29.10.2000, two males CL 7.9, 8.3 mm, 12 females CL 5.3–14.0 mm, one juvenile CL 4.3 mm (Dr C. Van Dover's collection).

South Barbados. Diapisub (DS *Nautile*), DS 04: site Orénoque A, 10°19.64'N, 58°53.33'W, 1697 m, 27 December 1992, one female CL 11.8 mm (MNHN-Na 15052).

Gulf of Guinea. Zaïrov (ROV *Victor*): dive 74-14, Régab site, west equatorial African margin, 05°47.80'S, 09°42.60'E, 3151 m, 27–28 December 2000, claw jaw, one female CL 16.8 mm (MNHN-Na 14277); same data, one female CL 18.5 mm (CBM-ZC 7042).

Biozaïre 1 (ROV *Victor*): dive 81-5, Régab site, 10 January 2001, slurp gun 1, one male CL 5.7 mm, two females CL 6.8, 13.2 mm, four juveniles CL 3.7–5.3 mm (MNHN-Na 14278).

Biozaïre 2 (ROV *Victor*): dive 146-9, Régab site, 28 November 2001, slurp gun 1, three females CL 16.5–21.0 mm (including one ovigerous female CL 21.0 mm) (Ifremer); same dive, slurp gun 2-1, seven males CL 7.4–11.0 mm, 14 females CL 5.8–23.0 mm (including two ovigerous females CL 14.5, 21.5 mm), nine juveniles CL 2.9–4.7 mm (Ifremer); same dive, slurp gun 2-2, seven males CL 6.0–9.2 mm, 18 females CL 7.8–23.0 mm, 12 juveniles



Figure 8. *Alvinocaris muricola* Williams, 1988. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) second to sixth abdominal somites, lateral (setae omitted); (D) telson and left uropod, dorsal (marginal setae on uropod omitted); (E) posterior part of telson, dorsal; (F) left antennal scale, dorsal (marginal setae omitted). Female from West Florida Escarpment (CL 13.8 mm; Dr C. Van Dover's collection).



Figure 9. *Alvinocaris muricola* Williams, 1988. (A) Carapace, dorsal; (B) left first pereopod, lateral; (C) chela of left first pereopod, inner; (D) left third pereopod, lateral; (E) dactylus and distal part of propodus of left third pereopod, lateral. Female from West Florida Escarpment (CL 13.8 mm; Dr C. Van Dover's collection).

CL 3.6–6.0 mm (Ifremer); dive 146–9, slurp gun 3, 20 males CL 5.3–15.7 mm, one juvenile CL 3.6 mm [Ifremer; one male and two females transferred to NHM (registration number 2004: 231–233); one male and three females to NSMT (registration number Cr 15776–15779); one male and two females to USNM (registration number 1020566); and one male and three females to ZMMU (registration number Ma 3303)]; dive PL 147-10, Régab site, 1 December 2001, slurp gun 1–1, one male CL 16.7 mm; slurp gun 1–2, two females CL 21.3, 21.4 mm (Ifremer); slurp gun 3, two males CL 7.6, 8.6 mm, 18 females CL 7.2–21.1 mm, three juveniles CL 4.2–5.0 mm (Ifremer); same dive, slurp gun 5-1, four males CL 7.1–8.8 mm, 10 females CL 7.2–20.4 mm, two juveniles CL 5.1, 5.2 mm (Ifremer); slurp gun 5-2, four males CL 7.1–11.8 mm, one female CL 20.5 mm (Ifremer).



Figure 10. *Alvinocaris muricola* Williams, 1988. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) carapace, dorsal; (D) third to sixth abdominal somites, lateral; (E) telson and right uropod, dorsal; (F) posterior part of telson, dorsal. Female from Régab site, west equatorial African margin (CL 16.8 mm; MNHN-Na 14277).



Figure 11. *Alvinocaris muricola* Williams, 1988. Variation in development and armature of rostrum. Specimens from Régab site, west equatorial African margin (Biozaïre 2). (A) Female, dive 146-09, slurp gun 3 (CL 11.0 mm; Ifremer); (B) female from same dive, slurp gun 2 (CL 21.0 mm; Ifremer); (C) female from same lot (CL 22.0 mm); (D) female from dive 147-10, slurp gun 1 (CL 21.6 mm; Ifremer); (E) male, dive 146, slurp gun 3 (CL 10.0 mm; Ifremer); (F) male (CL 16.2 mm; Ifremer); (G) male, dive 146, slurp gun 3 (CL 15.3 mm; Ifremer).



Figure 12. Alvinocaris muricola Williams, 1988. Plot of proportional length of rostrum (RL/CL) against carapace length (CL).

Bioz-Recup (RV *Suroit*): 2 km of Régab site,  $05^{\circ}47.16$ 'S,  $09^{\circ}41.99$ 'E, 3155 m, January 2003, MAC ("module autonome de colonisation") 10–147, three juveniles CL 3.8–4.8 mm (MNHN-Na 150539; MAC 10–151, two juveniles CL 3.8, 4.0 mm (MNHN-Na 15054); MAC 10–159, two juveniles CL 3.8, 4.4 mm (MNHN-Na 15055).

M 56 Cruise (RV *Meteor*): stn GeoB 8203-1, TV-grab, Congo Fan, 04°48.57'S, 09°54.51'W, 3110 m, 10 December 2002, four females CL 9.6–23.7 mm (SMF); stn GeoB 8212-2, TGV, Congo Fan, 04°48.56'S, 09°54.50'W, 3113 m, 17 December 2002, one ovigerous female (CL 21.3 mm) (SMF).

#### Description

Body moderately robust.

Rostrum (Figures 8A, 10A, 11A–G) directed forward, weakly curved dorsally or straight, 0.40–0.80 of carapace length in males, 0.30–0.65 in females, usually reaching to second segment of antennular peduncle in females, occasionally overreaching distal end of antennular peduncle in males; dorsal margin armed with 10–17 teeth, including 6–10 teeth on rostrum proper and four to six moderately large teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.34–0.40 of carapace length; ventral margin armed usually with 3–13 small teeth on anterior 0.30–0.70 (occasionally unarmed in large specimens with abnormally short rostrum). Carapace (Figures 8A, 9A, 10A, C) 0.69–0.83 times as wide as long; postrostral median ridge moderately high, extending to 0.75–0.80 of carapace length, dorsal angle about 155°; pterygostomian tooth strongly produced anteriorly in large specimens (CL>13 mm), far beyond tip of antennal tooth (Figures 8A, 10A, 11B, C, D, F); post-antennal groove relatively deep, almost parallel to horizontal plane of carapace; branchial region somewhat inflated, thus lateral face notably convex.

Third abdominal pleuron rounded (Figure 10D) or occasionally with one to four tiny teeth posteroventrally (Figures 8C, 13A). Fourth abdominal pleuron (Figures 8C, 10D, 13A) with one to four (most frequently two or three) posterolaterally. Fifth abdominal somite similarly armed with one strong posteroventral tooth and two to five additional smaller teeth. Sixth abdominal somite 1.50–1.70 times longer than height. Telson



Figure 13. *Alvinocaris muricola* Williams, 1988. (A) Third to fifth abdominal pleura, lateral (setae omitted); (B, D, F) chela of first pereopod, ventral (outer); (C, E, G) same, dorsal (inner); (H) entire first pereopod, lateral. Specimens from Régab site, west equatorial African margin. (A) Female from Zairov, dive 74-14 (CL 18.5 mm; CBM-ZC 7042); (B, C) female, Biozaïre 1, dive 81-5 (CL 13.2 mm; MNHN-Na 14278); (D, E) female from Zairov, dive 74-14 (CL 16.8 mm; MNHN-Na 14277); (F–H) female from Biozaïre 2, dive 146-09, slurp gun 2 (CL 21.0 mm; Ifremer).

(Figures 8D, 10E) nearly reaching to slightly overreaching posterior margin of uropodal endopod, length about 2.90–3.20 times anterior width and 4.90–5.20 times posterior width; armed with six to eight dorsolateral spines; posterior margin (Figures 8E, 10F) always moderately convex, armed with two pairs of spines at lateral angles and 12–14 plumose setae all longer than mesial pair of lateral spines.

Antennular peduncle (Figures 8B, 10B) moderately stout, second segment 1.90–2.10 times longer than wide. Antennal scale (Figures 2A, 8F) 0.48–0.51 of carapace length, 1.90–2.10 times longer than wide; lateral margin straight, slightly diverging anteriorly with dorsal median ridge; distolateral tooth moderately broad, directed forward, falling short of broadly rounded distal margin of blade.

First percopod strongly polymorphic as illustrated (Figures 9B, C, 13B–H); greatest height of palm at most 0.64 times length of chela; dactylus shorter than palm in adults. Third percopod (Figure 9D) moderately slender; dactylus (Figure 9E) with accessory spinules notably increasing in size distally; carpus 0.60–0.65 times as long as propodus; merus about 6.4 times as long as greatest height.

#### Size

Largest male CL 16.7 mm; largest female CL 21.5 mm, ovigerous females CL 14.5–21.5 mm. Maximal CL 23.6 mm, TL 83 mm.

#### Variation

As is apparent from the above description, the length and armature of the rostrum vary considerably in this species (see Figures 11A–G, 12), but they are seemingly affected occasionally by injury and regeneration. The rostrum is sometimes more elongate in males than in females.

The third abdominal pleuron is variable from smooth to bearing at most four tiny denticles (Figures 8C, 10D, 13A).

The first percopod exhibits considerable polymorphism, not correlated to sex (Figures 3C, 9B, C, 13B–H). A tendency for a decrease in the length of the fingers and an increase of the length and stoutness of the palm seem to be correlated to an increase in body size. The condition represented by Figure 13B and 13C is limited to juvenile and immature specimens.

#### Distribution

Previously known with certainty only from the type locality, cold seeps of the West Florida Escarpment in the Gulf of Mexico, at a depth of 3277 m (Figure 29). The present material represents new records of this species from south Barbados (tropical western Atlantic) and Régab (west equatorial African margin, 3113–3150 m). The specimen from Barbados significantly extends the bathymetric range to a shallower depth of 1697 m, and probably 1125 m (observation on video tapes).

#### Ecology

The Régab site, near the Zaïre Channel, where A. muricola was newly discovered, is characterized by a community dominated by bivalves including two large mytilid





Figure 14. (A) In situ photograph taken by the submersible *Nautile*, at a sulphide edifice of vent site Les Ruches, Snake Pit, Mid-Atlantic Ridge (3480 m) during Hydrosnake Cruise (PL 08): on the centre, one individual of *Alvinocaris markensis* Williams, 1988; other shrimps, *Chorocaris chacei*. Copyright Ifremer/Hydrosnake. (B) In situ photograph taken by the ROV *Victor*, at the cold seep site Régab, west equatorial African margin (3150 m) during Biozaïre 2 Cruise (PL 146): aggregation of *Alvinocaris muricola* Williams, 1988, among mytilid mussels *Bathymodiolus* sp. and tubeworm pogonophorans *Escarpia* n. sp.; lower left corner, coiled gastropods *Provanna* sp. (fide A. Warén, Stockholm). Copyright Ifremer/Biozaïre 2. (C) Same data, *Alvinocaris muricola* Williams, 1988, among mussels *Bathymodiolus* sp. and actiniarians; lower right corner, limpet gastropods *Paralepetopsis* sp. (fide A. Warén). Copyright Ifremer/Biozaïre 2.

Bathymodiolus spp. and vesicomyids (R. von Cosel, unpublished data), and vestimentiferans Escarpia n. sp. (Andersen et al. forthcoming). The communities are distributed in aggregates over an area of ca 1 km<sup>2</sup>. The substrata are mixed with soft reduced sediment and outcrops of carbonated concretions. The shrimps were over the mussel or the clam beds, or among the vestimentiferan Escarpia n. sp., or on the sediment (Figures 14A, B). Other accompanying species are present: sea-anemones, galatheid Munidopsis spp., gastropod Phymorhynchus sp., chiridotid holothurians and zoarcid fish. The highest densities of the shrimp were recorded on the mussel beds (more than 300 individuals per m<sup>2</sup>). The preliminary analysis of the stomach content of one specimen, using SEM, revealed the presence of fragments of diatoms and small foraminiferan drowned in dark mucus composed of very fine mineral particles. Four ovigerous females were collected; two carried 3774 and 1432 eggs, one was preserved intact and the fourth carried very few eggs. A small nematode, Chromadorita sp. (Adenophorea), occurs among the eggs (A. Vanreusel, unpublished data).

The photographs taken at cold seeps on the Congo Fan area during the M 56 Cruise, show that the faunal community is generally similar to that of Régab site, except that the mytilid bivalves are apparently absent. The following are found: vesicomyid clam beds composed of relatively few living individuals, dense cluster of vestimentiferan (probably a species of *Escarpia*), many galatheid lobsters, and chiridotid holothurians. *Alvinocaris muricola* lives overall among the *Escarpia* clusters, but also on the dark reduced sediment, occasionally covered with white bacteria mats.

The only specimen, collected from a subduction area with many mud volcanoes located on south Barbados accretionary prism (tropical western Atlantic), lives also on a bivalve community chiefly composed of two species of Bathymodiolus: B. boomerang Cosel and Olu, 1998 and B. sp. 1 (Cosel 2002) which are close to the species occurring on the African margin. In some active mud volcanoes, development of abundant communities composed of chemosynthetic species, vesicomyid bivalves and mytilid species Bathymodiolus boomerang and vestimentiferan worm Escarpia cf. laminata Jones, 1985, which characterize an area of high methane discharge. Other bathyal and rather opportunistic species were present, such as the serpulid polychaete Neovermilia sp., gastropods Phymorhynchus aff. alberti, geryonid crab Chaceon sp., lithodids Paralomis arethusa Macpherson, 1994 and Lithodes manningi Macpherson, 1994, and galatheid crabs (Olu et al. 1996; Warén and Bouchet 2001; Macpherson 1994). On the modiolid beds, Alvinocaris muricola were very abundant (more 300 individuals per m<sup>2</sup> on average), particularly on the Orénoque A site (1697 m). Analysis of the video tapes shows the occurrence of shrimps assignable to A. muricola on the El Pilar site (1125 m), which represents the shallowest bathymetric limit of this species at a depth of 1125 m. The deep mud volcano of Barbados, located some 400 km north from Barbados accretionary prism and at a depth of nearly 5000 m, was found to be colonized by bivalves *Calyptogena* sp., but no shrimp was observed there (K. Olu, personal communication).

## Remarks

The holotype and allotype of *A. muricola* are young, the carapace length measuring 6.4 mm in length in both specimens. Specific features are not differentiated in the type specimens. In this study, the specific identity of *A. muricola* is established primarily by using topotypic adult specimens from the West Florida Escarpment, kindly provided by Dr C. Van Dover. Comparison of the topotypic specimens with the material from Barbados and the west equatorial African margin has revealed that there are no morphological differences among the three well-separated populations. Therefore, we refer the Barbados and western African populations to *A. muricola*.

Although Williams (1988) mentioned that the obscurely serrated pleural margin of the third abdominal somite is diagnostic for *A. muricola*, our examination has shown that the condition of the pleural margin is quite variable in this species. Even in the holotype, the left margin bears a minute denticle ventrally, while the right margin is smooth, without trace of teeth or denticles. In the allotype, the left margin bears three small teeth posteroventrally; the right margin also bears two small teeth posteroventrally. The occasional presence of minute denticles or teeth on the third abdominal pleuron is also known in *A. markensis* and *A. longirostris* (present study; Kikuchi and Ohta 1995). As mentioned before, *A. muricola* is closely allied to *A. markensis*, *A. longirostris*, and *A. dissimilis* sp. nov. Differences among the four species are discussed under the account of *A. dissimilis* sp. nov.

Alvinocaris sp. represented by the allotype of A. stactophila is also similar to A. muricola. Nevertheless, the absence of ventral teeth on the rostrum and stouter second segment of the antennular peduncle seem to distinguish Alvinocaris sp. from A. muricola.

Shank et al. (1999) presented an unconfirmed report of A. muricola at Logatchev on the Mid-Atlantic Ridge at a depth of 3010 m by citing a personal communication from A. Gebruk and A. Vereshchaka, while they mentioned also the occurrence of A. markensis at the same site. Later Gebruk et al. (2000a) considered the Alvinocaris shrimp found on the mussel beds on the Anya's Garden site at Logatchev as an undescribed species. The authors related their species to A. muricola. However, the specific status of the Anya's Garden population remains unclear, as no material from the site has been available for study.

#### Alvinocaris stactophila Williams, 1988

(Figures 15–18, 29)

Alvinocaris stactophila Williams 1988, p 272 (part), Figures 5–7; Shank et al. 1999, p 246 (Table 1), 247 (Table 2), Figure 2; Kikuchi and Hashimoto 2000, p 146, 148 (key).

#### Material examined

Gulf of Mexico. *Johnson-Sea-Link*: dive 1879, Bush Hill hydrocarbon seep, about 129 km south of Louisiana, 27°46.94'N, 91°39.34'E, 534 m, 28 September 1986, one male CL 7.0 mm (holotype; USNM 234292).

Alvinocaris sp. 1 (allotype of A. stactophila), same data as for holotype of A. stactophila, one female CL 6.8 mm (USNM 23493).

#### Description

Body moderately robust for genus.

Rostrum (Figure 15A) directed forward, straight, 0.42 times as long as carapace, slightly reaching beyond distal margin of first segment of antennular peduncle; dorsal margin armed with 16 teeth, including eight teeth on rostrum proper and eight relatively small teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.28 of carapace length; ventral margin armed with one small subdistal tooth. Carapace (Figure 15A, B) with postrostral median ridge moderately high, extending to 0.60 of carapace length, dorsal angle 170°; pterygostomian tooth weakly produced anteriorly, slightly exceeding antennal tooth; post-antennal groove shallow; branchial region not particularly inflated.

Third abdominal pleuron unarmed (Figure 15C). Fourth abdominal pleuron with small posteroventral tooth and additional two or three tiny teeth on posterior margin. Fifth abdominal somite similarly armed with strong posteroventral tooth and additional three or four tiny teeth. Sixth abdominal somite 1.38 times longer than height. Telson (Figure 15D) reaching posterior margin of uropodal endopod, 3.00 times as long as anterior width and 4.70 times as long as posterior width; armed with six dorsolateral spines; posterior margin (Figure 15E) moderately convex, armed with eight pairs of spines (longest second pair noticeably curved mesially, mesial six pairs subequal in length).

Antennular peduncle (Figure 15B) moderately stout, second segment 1.80 times longer than wide. Antennal scale (Figure 16A) 0.46 times as long as carapace, 2.00 times longer than wide; lateral margin straight, slightly diverging anteriorly against dorsal median



Figure 15. *Alvinocaris stactophila* Williams, 1988. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) third to sixth abdominal somite, lateral; (E) telson and left uropod, dorsal; (F) posterior margin of telson, dorsal. Holotype male from Bush Hill hydrocarbon seep, Gulf of Mexico (534 m) (CL 7.0 mm; USNM 234291).



Figure 16. *Alvinocaris stactophila* Williams, 1988. (A) Left antennal scale, dorsal (marginal setae omitted); (B) left first pereopod, lateral; (C) chela of left first pereopod, outer; (D) left third pereopod, lateral; (E) dactylus and distal part of propodus of left third pereopod, lateral. Holotype male from Bush Hill hydrocarbon seep, Gulf of Mexico (534 m) (CL 7.0 mm; USNM 234291).

ridge; distolateral tooth directed forward, falling short of broadly rounded distal margin of blade.

First percopod (Figure 16B) as illustrated; greatest height of palm about 0.40 times length of chela (Figure 16C); dactylus longer than palm. Third percopod (Figure 16D) moderately slender; dactylus (Figure 16E) with strongly erect accessory spines on ventral margin, of which second and third accessory spines longer than distalmost accessory spine; carpus 0.66 times as long as propodus; merus 7.44 times as long as greatest height.

## Size

Only the male holotype has been available for study. CL 7.0 mm. TL ca 25 mm.



Figure 17. *Alvinocaris* sp 1. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal (left part of carapace deformed); (C) third to sixth abdominal somites, lateral; (D) telson and left uropods, dorsal (marginal setae on uropod omitted); (E) posterior margin of telson, dorsal. Allotype female of *Alvinocaris stactophila* Williams, 1988 from Bush Hill hydrocarbon seep, Gulf of Mexico (CL 6.8 mm; USNM 234293).



Figure 18. *Alvinocaris* sp. 1. (A) Right antennal scale, dorsal (marginal setae omitted); (B) right first pereopod, lateral; (C) chela of right first pereopod, outer; (D) right third pereopod, lateral; (E) dactylus and distal part of propodus of right third pereopod, lateral. Allotype female of *Alvinocaris stactophila* Williams, 1988 from Bush Hill hydrocarbon seep, Gulf of Mexico (CL 6.8 mm; USNM 234293).

## Distribution and habitat

Known with certainty only from the cold seep area at Louisiana Slope in the Gulf of Mexico (Figure 28), at a depth of 534 m.

## Remarks

Alvinocaris stactophila was described on the basis of nine specimens from the central Gulf of Mexico, of which the holotype male and allotype female have been available for study. The holotype differs from the allotype in several respects, although the sizes are similar to one another (CL 7.0 mm in the holotype, 6.8 mm in the allotype). The ventral margin of the rostrum is armed with one tiny subdistal tooth in the holotype (Figure 15A), while in the allotype it is unarmed (Figure 17A). The fourth abdominal pleuron bears three (left) or four (right) teeth on the posterior margin (including the posteroventral tooth) in the holotype (Cf. Figure 15C), but it is only bluntly pointed at the posteroventral angle in the allotype (Figure 17C). The posterior margin of the telson is armed with eight pairs of spines, of which the second pair are longest and mesially curved in the holotype (Figure 15E), rather than having two pairs of lateral spines and 12 long plumose setae in the allotype (Figure 17E). The second segment of the antennular peduncle is more slender in the holotype (Figure 15B, 17B). The chela of the first pereopod in the

male holotype is much stouter than in the female allotype (Figures 16B, C, 18B, C). The third to fifth percopods are more slender in the holotype than in the allotype (Figures 16D, 18D). The accessory spines on the dactylus of the third percopods of the holotype are more strongly erect, of which the second and third spines are longer than the distalmost spine (Figure 16E). In the allotype, the accessory spines are less erect and increase in length distally (Figure 18E). Although only two specimens have been available for comparison, the differences in the armature on the posterior margin of the telson and the armature of the dactylus of the third percopod, at least, strongly suggest that they represent two separate species. Therefore, the allotype is here treated as a species of uncertain taxonomic status. A final decision will be made when an adequate series of adult specimens from the Gulf of Mexico is available for study. Here *A. stactophila* is re-diagnosed on the basis of the holotype.

As mentioned before, the possession of spines other than two lateral pairs on the posterior margin of the telson links *A. stactophila* to *A. lusca* and *A. brevitelsonis*. Differences among the three species are discussed under "Remarks" for *A. lusca*.

Alvinocaris stactophila somewhat resembles A. williamsi particularly in the short rostrum. Other than the armature on the posterior margin of the telson, the less stout antennular peduncle and the fourth abdominal pleuron armed with more than one posterolateral tooth distinguish A. stactophila from A. williamsi.

## Alvinocaris longirostris Kikuchi and Ohta, 1995 (Figures 19, 20, 29)

Alvinocaris sp.: Ohta 1990, Figure 6; Kim and Ohta 1991, Figures 7, 9.

Alvinocaris longirostris Kikuchi and Ohta 1995, p 772, Figures 1–7 [type locality: Clam site on the Iheya Ridge, Okinawa Trough, 27°32.70'N, 126°58.20'E, 1360 m]; *Fujikura* et al. 1995, p 231 (Table 1), 232, 233 (Table 2), 234; Fujikura et al. 1996, p 136 (Table 1), 142; Hashimoto 1997, p 190; Watabe and Miyake 2000, p 32, Figure 4.

## Material examined

Okinawa Trough. DS *Shinkai* 2000: dive #1094, north-eastern slope of Iheya Ridge, 27°47.179'N, 126°54.091'E, 1053 m, 8 May 1999, coll. S. Tsuchida, seven females CL 8.1–16.9 mm (JAMSTEC 15968–15974).

## Description

Body relatively robust.

Rostrum (Figure 19A, B) directed forward or very slightly downward, nearly straight or slightly curved dorsally, 0.64–0.98 times carapace length, overreaching distal margin of second segment of antennular peduncle, sometimes overreaching distal margin of third segment; dorsal margin armed with 9–15 teeth, including 5–10 teeth on rostrum proper and four to seven relatively large teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.38–0.48 of carapace length; ventral margin armed with four to nine small teeth on anterior 0.30–0.40. Carapace (Figures 19A, 20A) 0.65–0.72 times as wide as long; postrostral median ridge high, extending to 0.75–0.80 of carapace length, dorsal angle about 150°; pterygostomian tooth strongly produced anteriorly, far exceeding antennal tooth; post-antennal groove shallow; branchial region not particularly inflated.



Figure 19. *Alvinocaris longirostris* Kikuchi and Ohta, 1995. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) third to sixth abdominal somites, lateral; (D) telson and right uropod, dorsal (marginal setae on uropod omitted); (E) posterior margin of telson, dorsal. Female from Iheya Ridge, Okinawa Trough (CL 17.9 mm; JAMSTEC).



Figure 20. *Alvinocaris longirostris* Kikuchi and Ohta, 1995 (A) Carapace, dorsal; (B) left antennal scale, dorsal (marginal setae omitted); (C) left first pereopod, lateral; (D) chela of left first pereopod, outer; (E) left third pereopod, lateral; (F) dactylus and distal part of propodus of left third pereopod, lateral. Female from Iheya Ridge, Okinawa Trough (CL 17.9 mm; JAMSTEC).

Third abdominal pleuron smooth or with few minute denticles. Fourth abdominal pleuron (Figure 19C) with one to four small teeth posterolaterally. Fifth abdominal somite similarly armed with one strong posteroventral tooth and additional two to five small teeth. Sixth abdominal somite 1.50–1.70 times longer than proximal height. Telson (Figure 19D) falling slightly short of or reaching posterior margin of uropod, length about 2.53–2.80 times anterior width and 4.10–4.90 times posterior width; armed with five to seven dorsolateral spines on either side; posterior margin (Figure 19E) always moderately convex, armed with two pairs of spines at lateral corner and 12–14 plumose setae all longer than mesial pair of lateral spines.

Antennular peduncle (Figure 19B) relatively stout, second segment 1.58–1.69 times longer than wide. Antennal scale (Figure 20B) about half length of carapace, 1.72–1.90 times longer than wide; lateral margin straight or slightly concave, somewhat diverging against dorsal median ridge; distolateral tooth directed rather laterally, falling short of broadly rounded distal margin of blade.

First percopod (Figure 20C) as illustrated; greatest height of palm about 0.40 times length of chela (Figure 20D); dactylus (Figure 20D) longer than palm. Third percopod (Figure 20E) moderately slender; dactylus (Figure 20F) with accessory spinules increasing in size distally; carpus 0.60–0.65 times as long as propodus; merus 6.00–6.40 times as long as greatest height.

#### Size

Males were not available for study. Largest female CL 16.9 mm; TL ca 70 mm.

#### Variations

Variation in the armature of the pleuron of the third to fifth abdominal somites and the polymorphism of the first pereopod were described and figured by Kikuchi and Ohta (1995).

#### Distribution and habitat

Known from hydrothermally influenced areas in the Okinawa Trough (Figure 29): Iheya Ridge, at depths of 1053–1410 m; Hatoma Knoll, at depths of 1454–1627 m (Kikuchi and Ohta 1995; Watabe and Miyake 2000; Ohta and Kim 2001). Also known from cold seeps at Off Hatsushima site, Sagami Bay, at depths of 1120–1220 m (Fujikura et al. 1995). This is the sole representative of the Alvinocarididae that occurs both on hot vents and cold seeps.

## Remarks

The type material was not re-examined, as the supplemental specimens from Iheya Ridge have been available for study. In the original description (Kikuchi and Ohta 1995), *Alvinocaris longirostris* was characterized by the proportionally long rostrum which overreaches the distal end of the antennular peduncle, a relatively long stylocerite reaching to the midlength of the ultimate segment of the antennular peduncle, and the pattern of the armature of the second to fifth pereopods (Kikuchi and Ohta 1995). Among these characters, only the rostrum is still useful in characterizing the species, although interspecific overlap is observed between *A. longirostris*, *A. markensis*, and *A. muricola*. The length of the stylocerite is not useful in characterizing *A. longirostris* because of intraspecific variation. As mentioned before, the armature of the second to fifth pereopods is not useful. Differences between *A. longirostris* and similar species are discussed under "Remarks" for *A. dissimilis* sp. nov.

Fujikura et al. (1995, 1996) reported the occurrence of *A. longirostris* at cold seeps in Sagami Bay, central Japan, Off Hatsushima site. The identification of the voucher specimens from Sagami Bay was made by Dr T. Kikuchi (Fujikura et al. 1995, 1996), who described this species (Kikuchi and Ohta 1995). It is remarkable that the site is a cold seep, although *A. longirostris* was originally described from hot vents. So far, there is no other

alvinocaridid species that occurs on both hot vents and cold seeps. Nevertheless, Fujikura et al. (1996) recorded two further vent species known from Okinawa Trough, provannid gastropod *Provanna glabra* Okutani, Tsuchida and Fujikura, 1992 and mytilid *Bathymodiolus japonicus* Hashimoto and Okutani, 1994 from Off Hatsushima site. They indicated the existence of high temperature anomalies at Off Hatsushima site. The authors also mentioned that no shrimp species was found at cold seeps on the Okinoyama Bank, about only 40 km east of Off Hatsushima site. Considering the rare occurrence of *A. longirostris* at Off Hatsushima site and the absence of the shrimp at the Okinoyama Bank, it is reasonable to consider that *A. longirostris* is primarily associated with vent environments.

## Alvinocaris brevitelsonis Kikuchi and Hashimoto, 2000 (Figures 21, 22, 29)

Alvinocaris brevitelsonis Kikuchi and Hashimoto 2000, p 136 (part), Figures 1, 2 [type locality: Depression C, Minami-Ensei Knoll, Okinawa Trough, 28°23.35'N, 127°38.38'E, 705 m].

## Material examined

Okinawa Trough. DS *Shinkai* 2000: dive 547, Depression C, Minami-Ensei Knoll, 28°23.35'N, 127°38.38'E, 705 m, 3 June 1991, suction sampler, coll. J. Hashimoto, one ovigerous female CL 13.8 mm (holotype; NSMT-Cr 12454).

## Description

Body moderately robust.

Rostrum (Figure 21A, B) directed forward, slightly curved dorsally, 0.55 times carapace length, reaching distal margin of second segment of antennular peduncle; dorsal margin armed with 13 teeth, including eight teeth on rostrum proper and five relatively large teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.38 of carapace length; ventral margin armed with seven small teeth on anterior 0.60. Carapace (Figure 21A, C) 0.70 times as wide as long; postrostral median ridge high, extending to 0.70 of carapace length, dorsal angle about 150°; pterygostomian tooth weakly produced anteriorly, subequal in size to antennal tooth, slightly exceeding antennal tooth; post-antennal groove obsolete; branchial region not particularly inflated.

Third abdominal pleuron unarmed. Fourth abdominal pleuron (Figure 21D) with three tiny teeth on posteroventral margin. Fifth abdominal pleuron with strong posteroventral tooth and one additional tooth on posterior margin. Sixth abdominal somite 1.40 times longer than proximal height. Telson (Figure 21E) falling somewhat short of posterior margin of uropodal endopod, length 2.70 times anterior width and 4.30 times posterior width; armed with six or seven dorsolateral spines; posterior margin (Figure 21F) moderately convex, armed with six pairs of spines (second pair longest and third pair shortest) and two pairs of plumose setae subequal in length to longest second spine.

Antennular peduncle (Figure 21B) moderately stout, second segment 1.80 times as long as wide. Antennal scale (Figure 22A) half length of carapace, 1.87 times longer than wide; lateral margin straight, weakly diverging anteriorly against dorsal median ridge; distolateral tooth moderately broad, directed anteriorly, not reaching broadly rounded distal margin of blade.

First percopod (Figure 22B) as illustrated; greatest height of palm 0.48 length of chela (Figure 22C); dactylus (Figure 22C) subequal in length to palm. Third percopod



Figure 21. *Alvinocaris brevitelsonis* Kikuchi and Hashimoto, 2000. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) carapace, dorsal; (D) third to sixth abdominal somites, lateral; (E) telson and left uropod, dorsal; (F) posterior margin of telson, dorsal. Holotype ovigerous female from Minami Ensei Knoll, Mid-Okinawa Trough (CL 13.8 mm; NSMT-Cr 12454).



Figure 22. *Alvinocaris brevitelsonis* Kikuchi and Hashimoto, 2000. (A) Right antennal scale, dorsal (marginal setae omitted); (B) right first pereopod, lateral; (C) chela of right first pereopod, outer; (D) right third pereopod, lateral; (E) dactylus and distal part of propodus of right third pereopod, lateral. Holotype ovigerous female from Minami Ensei Knoll, Mid-Okinawa Trough (CL 13.8 mm; NSMT-Cr 12454).

(Figure 22D) moderately slender; dactylus (Figure 22E) with accessory spinules increasing in size distally; carpus 0.68 times as long as propodus; merus about 7.30 times as long as greatest height.

Size

Only the ovigerous female holotype is known for this species. CL 13.8 mm. TL ca 57 mm.

## Distribution and habitat

Known only from the type locality in Minami-Ensei Knoll (Figure 29), at a depth of 705 m. This species occurs at a hydrothermally influenced area. *Alvinocaris dissimilis* sp. nov. and *Shinkaicaris leurokolos* comb. nov. occurred sympatrically.

#### Remarks

Re-examination of the type series and some of the non-type specimens referred to *A. brevitelsonis* by Kikuchi and Hashimoto (2000) has disclosed that two species of *Alvinocaris*, one unidentified species of *Opaepele* and *Shinkaicaris leurokolos* comb. nov. were confounded by these authors. The paratypes of *A. brevitelsonis* and non-type specimens referred to *A. brevitelsonis* are here assigned to *A. dissimilis* sp. nov. This new species is readily separated from *A. brevitelsonis* by having far fewer ventral teeth on the rostrum and by the setal fringe of the posterior margin of the telson. So far, *A. brevitelsonis* is represented only by the holotype.

The possession of more than two pairs of spines on the posterior margin of the telson links *A. brevitelsonis* to *A. lusca* and *A. stactophila*. As Kikuchi and Hashimoto (2000) correctly pointed out, the shorter telson, which falls short of the posterior end of the uropod, distinguishes *A. brevitelsonis* from *A. lusca*. Other differences among the three species are discussed under "Remarks" for *A. lusca*.

It is interesting to compare *A. brevitelsonis* with *A. longirostris* because of their superficial similarity and the proximity of the known localities. Other than the armature of the posterior margin of the telson, *A. brevitelsonis* differs from *A. longirostris* in the less produced pterygostomian tooth of the carapace.

Alvinocaris williamsi Shank and Martin, 2003

(Figures 23, 24, 29)

Alvinocaris n. sp. 2: Shank et al. 1999, p 246, Table 1. Alvinocaris williamsi Shank and Martin 2003, p 159, Figures 1–3.

#### Material examined

Mid-Atlantic Ridge. Saldanha: dive 1274, Menez Gwen, 37°51.60'N, 33°31.35'W, 865 m, 15 July 1998, SMAC tray, one female CL 14.4 mm (MNHN-Na 15056).

Diva 1: dive 14, Menez Gwen,  $37^{\circ}50.46$ 'N,  $31^{\circ}31.35$ 'W, 845 m, 22 May 1994, one female CL 8.0 mm (MNHN-Na 15057); same data, one male CL 4.6 mm, one female CL 6.3 mm (CBM).

Diva 2: dive 12, Menez Gwen, 37°50.54'N, 31°31.30'W, 866 m, 14 June 1994, slurp gun, one juvenile CL 3.5 mm (MNHN-Na 15058); dive 13, same site, 15 June 1994, one female CL 8.1 mm (MNHN-Na 15059); dive 14, same site, 19 June 1994, one male CL 6.1 mm (MNHN-Na 15060); dive 16, same site, 22 June 1994, slurp gun, three females CL 5.0–8.8 mm (including one ovigerous CL 5.8 mm) (MNHN-Na 15061); dive 26, same site, 2 July 1994: one male CL 5.0 mm (MNHN-Na 15062).

#### Description

Body most robustly built among species of Alvinocaris presently known.

Rostrum (Figure 23A, B) directed forward, straight, 0.27–0.37 of carapace length, slightly falling short of or slightly overreaching distal margin of first segment of antennular peduncle; dorsal margin armed with 10–15 teeth, including five to nine teeth on rostrum proper and four to eight small to moderately large teeth on carapace posterior to orbital margin, posteriormost tooth arising from 0.13–0.20 of carapace length; ventral margin always unarmed. Carapace (Figures 23A, 24A) about 0.70 times as wide as long; postrostral median ridge relatively low, only weakly compressed laterally, extending to



Figure 23. *Alvinocaris williamsi* Shank and Martin, 2003. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) third to sixth abdominal somites, lateral; (D) telson and left uropod, dorsal; (E) posterior margin of telson, dorsal. Female from Menez Gwen, Mid-Atlantic Ridge (CL 14.4 mm; MNHN-Na 15056).



Figure 24. *Alvinocaris williamsi* Shank and Martin 2002. (A) Carapace, dorsal; (B) left first pereopod, lateral; (C) chela of left first pereopod, outer; (D) left third pereopod, lateral; (E) dactylus and distal part of propodus of left third pereopod, lateral. Female from Menez Gwen, Mid-Atlantic Ridge (CL 14.4 mm; MNHN-Na 15056).

midlength of carapace, with dorsal angle 150°; pterygostomian tooth somewhat produced anteriorly, subequal in size to antennal tooth, projecting distinctly beyond antennal tooth; post-antennal groove obsolete; branchial region not inflated.

Third abdominal pleuron unarmed. Fourth abdominal pleuron (Figure 23C) rounded or with small posteroventral tooth. Fifth abdominal pleuron armed with strong posteroventral tooth and two to four additional tiny teeth on posterior margin. Sixth abdominal somite 1.10–1.20 times longer than height. Telson (Figure 23D) not reaching posterior margin of uropodal endopod, length 2.20–2.30 times as long as anterior width and 3.10–4.00 times as long as posterior width; armed with six or seven dorsolateral spines arranged in straight or slightly convex line; posterior margin (Figure 23E) broadly rounded (occasionally with shallow median notch), armed with two pairs of lateral spines and 14–16 plumose setae all longer than mesial pair of lateral spines.

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Antennular peduncle (Figure 23B) very stout, second segment 1.05–1.11 times longer than wide. Antennal scale (Figure 23B) 0.40–0.43 times as long as carapace, 1.40–1.50 times longer than wide; lateral margin straight or convex; distolateral tooth broad, directed forward, not reaching broadly rounded distal margin of blade.

First percopod (Figure 24B) as illustrated; greatest height of palm at most 0.50 times length of chela (Figure 24C); dactylus (Figure 24C) subequal in length to palm. Third percopod (Figure 23D) relatively stout; dactylus (Figure 24E) with accessory spinules notably increasing in size distally; carpus 0.65 times as long as propodus; merus about 5.50 times as long as greatest height.

## Size

Largest male CL 6.1 mm; largest female 10.3 mm, ovigerous female 5.8 mm.

## Distribution and habitat

Known only from hot vents at Menez Gwen site on the Mid-Atlantic Ridge (Figure 29), at depth of 850–865 m. It was difficult to find shrimps from the submarine or image on the video tapes, but the specimens used in this study were collected from the mussel beds of the mytilid *Bathymodiolus azoricus* Cosel, Comtet and Krylova, 1999.

## Remarks

Alvinocaris williamsi is clearly distinguished from most others in the genus by the robust body, relatively short rostrum usually unarmed on the ventral margin, relatively low postrostral median ridge on the carapace reaching only to the midlength of the carapace, the posteriormost median tooth on the carapace arising from the anterior 0.13–0.20 of the carapace, broad telson and very stout antennular peduncle. Two other species of *Alvinocaris* also have similarly short rostra with ventral margins unarmed or armed only with one tooth, *A. stactophila* and *Alvinocaris* sp. 1. However, the latter two differ from *A. williamsi* in the less robust body, narrower telson and more slender antennular peduncle. The presence of a row of plumose setae on the posterior margin of the telson, instead of a row of spines, distinguishes *A. williamsi* from *A. stactophila*.

Some of the characters mentioned above are useful in discriminating juveniles of A. williamsi from those of the other species. These include the relatively robust sixth abdominal somite (1.30 times as long as high versus 1.40 or more times as long) and more stout second segment of the antennular peduncle (about 1.30 times as long as wide versus more than 1.50 times as long).

#### Alvinocaris dissimilis sp. nov.

(Figures 25, 26, 29)

Alvinocaris brevitelsonis Kikuchi and Hashimoto 2000, p 136 (part), Figure 3a-g. See "Remarks".

## Material examined

Okinawa Trough. DS *Shinkai* 2000: dive 547, Depression C, Minami Ensei Knoll, 28°23.35'N, 127°38.38'E, 705 m, 3 June 1991, suction sampler, coll. J. Hashimoto, one ovigerous female CL 9.7 mm (holotype; NSMT-Cr 15787); same data, one male 6.9 mm



Figure 25. *Alvinocaris dissimilis* sp. nov. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) third to sixth abdominal somites, lateral; (D) telson and left uropod, dorsal (marginal setae on uropod omitted); (E) posterior margin of telson, dorsal. Holotype ovigerous female from Minami-Ensei Knoll, Mid-Okinawa Trough (CL 11.9 mm; NSMT-Cr 15787).



Figure 26. *Alvinocaris dissimilis* sp. nov. (A) Carapace, dorsal; (B) left antennal scale, dorsal (marginal setae omitted); (C) left first pereopod, lateral; (D) chela of left first pereopod, outer; (E) left third pereopod, lateral; (F) dactylus and distal part of propodus of left third pereopod, lateral. Holotype ovigerous female from Minami-Ensei Knoll, Mid-Okinawa Trough (CL 11.9 mm; NSMT-Cr 15787).

(paratype; NSMT-Cr 12456); same data, one ovigerous female CL 7.3 mm (paratype; NSMT-Cr 15788); same data, four males CL 5.1–8.4 mm (non-types; Dr T. Kikuchi's collection).

## Description

## Body moderately robust.

Rostrum (Figure 25A, B) directed forward, straight or very slightly curved dorsally, 0.53–0.61 of carapace length, usually reaching to second segment of antennular peduncle (rarely slightly overreaching distal margin of second segment); dorsal margin armed with 13–17 teeth, including 8–10 teeth on rostrum proper and five to eight relatively small teeth

on carapace posterior to orbital margin, posteriormost tooth arising from 0.19–0.31 of carapace length; ventral margin armed with one or two small subdistal teeth. Carapace (Figures 25A, 26A) width 0.65–0.80 of length; postrostral median ridge moderately high, extending to 0.60–0.70 of carapace length, dorsal angle about 155°; pterygostomian tooth weakly produced anteriorly, larger than antennal tooth, slightly exceeding antennal tooth; post-antennal groove shallow; branchial region not particularly inflated.

Third abdominal pleuron unarmed. Fourth abdominal pleuron (Figure 25C) with small posteroventral tooth and additional one or two teeth on posterior margin. Fifth abdominal somite similarly armed with strong posteroventral tooth and additional one to five tiny teeth on posterior margin or ventral margin. Sixth abdominal somite 1.30–1.40 times longer than height. Telson (Figure 25D) not reaching posterior margin of uropodal endopod, 2.70–2.90 times as long as anterior width and 4.30–4.60 times as long as posterior width; armed with five to eight dorsolateral spines; posterior margin (Figure 25E) convex (rarely shallowly notched medially), armed with two pairs of spines at lateral corners and 12–14 plumose setae all longer than mesial pair of lateral spines.

Antennular peduncle (Figure 25B) stout, second segment 1.43–1.78 times longer than wide. Antennal scale (Figure 26B) 0.48–0.52 times as long as carapace, 1.90–2.16 times longer than wide; lateral margin straight, slightly converging against dorsal median ridge; distolateral tooth slender, directed forward, falling short of broadly rounded distal margin of blade.

First percopod as illustrated (Figure 26C); greatest height of palm at most 0.40 times length of chela (Figure 26D); dactylus (Figure 26D) longer than palm. Third percopod (Figure 26E) moderately slender; dactylus (Figure 26F) with accessory spinules notably increasing in size distally; carpus 0.60–0.65 times as long as propodus; merus about 6.4 times as long as greatest height.

#### Size

Largest male CL 8.4 mm; largest female CL 9.8 mm, ovigerous females CL 7.3–9.8 mm. Maximal TL ca 41 mm.

## Variation

Variation in the rostral shape and dentition was illustrated by Kikuchi and Hashimoto (2000, Figure 3a-g, as *Alvinocaris brevitelsonis*).

## Distribution and habitat

Known only from Minami-Ensei Knoll, Mid-Okinawa Trough (Figure 28), at a depth of 705 m. This new species occurs in a hydrothermally active area. *Alvinocaris brevitelsonis* and *Shinkaicaris leurokolos* comb. nov. occurred sympatrically with *A. dissimilis* (cf. Kikuchi and Hashimoto 2000).

## Etymology

From the Latin *dissimilis* (different), indicating that this new species is quite different from *A. brevitelsonis*, with which the new species was confused in the original description.

## Remarks

Re-examination of the type series of *A. brevitelsonis* disclosed that two species were confounded, one of which is described as new, *A. dissimilis* sp. nov. The true *A. brevitelsonis* is known only by the holotype. Furthermore, it has been found that non-type material referred to as *A. brevitelsonis* by Kikuchi and Hashimoto (2000) contains three species, *A. dissimilis, Shinkaicaris leurokolos* comb. nov. (cf. Kikuchi and Hashimoto 2000, Figure 3i), and *Opaepele* sp. (cf. Kikuchi and Hashimoto 2000, Figure 3h). *Opaepele* sp. is generally similar to *Opaepele loihi* Williams and Dobbs, 1995, but more careful comparison is needed to determine the specific status.

Alvinocaris dissimilis sp. nov., A. markensis, A. muricola, and A. longirostris are morphologically very similar to one another. These four species share the rostrum reaching at least to the second segment of the antennular peduncle and armed usually with one or more ventral teeth, relatively high postrostral median ridge on the carapace, and the posterior margin of the telson with long plumose setae and two lateral pairs of spines. The differences among these four species are summarized in Table II. These characters should be used with caution, as most of them are useful only for adult specimens.

Although the proportional length and armature of the rostrum are highly variable in A. muricola (see Figures 8, 10, 11), the rostral characters are still useful for species discrimination. Female specimens of A. longirostris can be separated from females of A. muricola and both females and males of A. markensis by the proportionally longer rostrum (0.64–0.98 times as long as the carapace versus 0.30–0.70 times as long), which reaches or overreaches the anterior end of the antennular peduncle. The number of dorsal teeth on the rostrum (including those on the carapace) tends to be fewer in A. longirostris than in A. markensis and A. dissimilis (9–15 in the former versus 13–19 in the latter), although there is a partial overlap; the number greatly overlaps between A. longirostris and A. muricola. The ventral teeth of the rostrum are fewest in A. dissimilis sp. nov. among the

	A. markensis	A. muricola	A. longirostris	A. dissimilis sp. nov.
Rostral length/carapace length	0.45–0.70	0.40–0.80 (males), 0.30–0.65 (females)	0.64–0.98	0.53–0.61
Rostral dorsal teeth	14-19	10–17	9-15	13-17
Rostral ventral teeth	6–9	Usually 3-13	4-9	0–2
Position of posteriormost median tooth on carapace	0.24–0.31	0.34-0.40	0.38-0.48	0.19–0.31
Carapace width/length	0.52-0.65	0.69-0.83	0.65 - 0.72	0.65-0.70
Antennal groove on carapace	Shallow	Relatively deep	Shallow	Shallow
Pterygostomian angle of carapace	Strongly produced	Strongly produced	Strongly produced	Moderately produced
Anterior part of branchial region of carapace	Slightly convex	Strongly convex	Slightly convex	Slightly convex
Penultimate segment of antennular peduncle length/ width	1.79–2.05	1.90-2.10	1.58–1.69	1.43–1.78
Antennal scale length/width Distolateral tooth of antennal scale	1.91–2.04 Directed forward	1.90–2.10 Directed forward	1.72–1.90 Somewhat directed anterolaterally	1.91–2.16 Directed forward

Table II. Summary of morphological differences among Alvinocaris markensis Williams, 1988, A. muricola Williams, 1988, A. longirostris Kikuchi and Ohta, 1995, and A. dissimilis sp. nov.

four species compared (0-2 versus 4-13). However, the abnormality exhibited by *A. muricola* (the ventral margin of the rostrum is occasionally unarmed in large specimens with abnormally short rostra) diminishes the significance of this character.

The more posteriorly arising posteriormost dorsal tooth on the carapace is useful to distinguish *A. longirostris* from *A. markensis* and *A. dissimilis* sp. nov. In *A. longirostris*, the posteriormost tooth arises from 0.38–0.48 of the carapace length, while it is situated at 0.24–0.31 of the carapace length in *A. markensis*, 0.19–0.31 in *A. dissimilis*. The tooth tends to arise more posteriorly in *A. muricola* than in *A. markensis* and *A. dissimilis* (0.34–0.40 versus 0.19–0.31).

Adult specimens of *A. muricola* are characteristic in the somewhat inflated, notably convex branchial region of the carapace. Thus the ratio "carapace width/carapace length" is greater in *A. muricola* than in *A. markensis* and *A. longirostris*.

The post-antennal groove is more conspicuous in A. muricola than in the other three species.

The pterygostomian tooth of the carapace is less produced in A. dissimilis than in the other three species.

The second segment of the antennular peduncle is stouter in *A. dissimilis* sp. nov. and *A. longirostris* than in *A. markensis* and *A. muricola* (the ratios length/width are 1.43–1.78 in *A. dissimilis* sp. nov., 1.72–1.90 in *A. longirostris*, 1.79–2.05 in *A. markensis* and 1.90–2.10 in *A. muricola*).

The antennal scale may be broader in *A. longirostris* than in the other three species (1.72–1.90 times as long as wide versus 1.90–2.16 as long). Furthermore, the distolateral tooth of the antennal scale is somewhat directed anterolaterally in *A. longirostris*, rather than directed forward in the other three species.

Alvinocaris dissimilis sp. nov. also resembles Alvinocaris sp. 1, represented by the allotype of A. stactophila. In A. dissimilis sp. nov., the ventral margin of the rostrum is armed with one or two teeth or occasionally unarmed (Kikuchi and Hashimoto 2000, as A. brevitelsonis). In Alvinocaris sp. 1, the ventral margin of the rostrum is unarmed. Alvinocaris dissimilis sp. nov. differs from Alvinocaris sp. 1 in the relatively long rostrum reaching the distal margin of the second segment of the antennular peduncle. Furthermore, the accessory spinules on the dactylus of the third pereopod are stouter in A. dissimilis sp. nov. than in Alvinocaris sp. 1 (cf. Figures 26F, 18E). Examination of additional adult specimens will eventually reveal more differences between the two species.

#### Indeterminate or unnamed species

As mentioned before, four undescribed or indeterminate species of *Alvinocaris*, other than *Alvinocaris* sp. 1 represented by the allotype of *A. stactophila*, have been recorded in the world. Shank et al. (1999) mentioned the existence of an undescribed species from the Edison Seamount in the Bismarck Sea, western Pacific (1483 m). This undescribed species (here referred to *Alvinocaris* sp. 2) is now under study by K. Baba and M. Türkay (K. Baba 2002, personal communication). Our preliminary examination of the material from the Lau Basin in the south-western Pacific (1750–2750 m) suggests the existence of the same species in these localities. The latter material will be reported formally after Baba and Türkay's paper is published.

Recently, two species of *Alvinocaris* were discovered from volcanic slopes and hot vents on the Brothers and Rumble seamounts, north of Bay of Plenty, New Zealand, although the two are not named yet. These two species (here referred to *Alvinocaris* sp. 3 and *Alvinocaris* sp. 4) are under study by R. Webber and J. C. Yaldwyn (Webber and Bruce 2002; R. Webber, personal communication).

Van Dover et al. (2003) reported the occurrence of an indeterminate species of *Alvinocaris* (here referred to *Alvinocaris* sp. 5) on methane seeps of the Blake Ridge Diapir, north-western Atlantic (2155 m). The authors suggested that the species was similar to *A. muricola*, but that the degree of morphological differences found in the number, position and length of the telson setae, and the presence of a prominent spine on the third maxilliped were sufficient to warrant a description of a new species. Personal examination of specimens from the Blake Ridge kindly provided by C. L. Van Dover has shown that the differences suggested by Van Dover et al. (2003) are not reliable, but other characters derived from the rostrum and antennular peduncle are useful to separate *Alvinocaris* sp. 5 from *A. muricola*. Material from the Blake Ridge will be dealt with in a separate paper.

#### Shinkaicaris gen. nov.

## Type species

Alvinocaris leurokolos Kikuchi and Hashimoto, 2000. Original designation by monotypy.

## Diagnosis

Rostrum well developed, compressed laterally, always with dorsal teeth extending to anterior part of carapace. Carapace not extremely inflated, with moderately large antennal and large pterygostomian tooth; antennal tooth distinctly buttressed, suborbital margin of carapace just mesial to antennal tooth forming conspicuous lobe; post-antennal groove shallow, but distinct. Fourth and fifth abdominal pleura dentate posterolaterally. Telson with dorsolateral spines arranged in sinuous rows; posterior margin convex, with two pairs of lateral spines and row of numerous plumose setae. Eyes lacking corneal facets, but with diffused pigmentation inside, broadly fused mesially; anterior surface without tubercle. Antennal scale broadly oval, not locked with antennule. Third maxilliped to fourth pereopods without strap-like epipods. Ischium of second pereopod lacking ventrolateral spine. Dactyli of third to fifth pereopods somewhat compressed laterally, each with three or four rows of accessory spines on ventral margin; meri and ischia of third to fifth pereopods unarmed. Branchial formula identical to that of *Alvinocaris*. Second to fourth pleopods each with slender, simple appendix interna in both sexes; fifth pleopod with well-developed appendix interna bearing terminal cluster of cincinnuli.

## Remarks

Shinkaicaris leurokolos is superficially similar to species of Alvinocaris in the laterally compressed, dorsally dentate rostrum, a plesiomorphic feature within the Alvinocarididae. Presumably apomorphic characters in S. leurokolos, such as the broadly fused eyes, sinuous rows of the dorsolateral spines on the telson, the possession of three or more rows of accessory spines on the ventral surfaces of the dactyli of the third to fifth pereopods, and the unarmed ischium of the second to fifth pereopods, are shared by Chorocaris, Opaepele, and Rimicaris. Although Kikuchi and Hashimoto (2000) reported the presence of a spiniform

tubercle on the anterior surface of the eye in *S. leurokolos*, our re-examination of the type series has shown that there is no spiniform tubercle on the eye. The distinctly buttressed antennal tooth and the presence of a small rounded lobe on the suborbital margin of the carapace are unique for *S. leurokolos* among alvinocaridids. *Shinkaicaris* is further distinguished from the fifth alvinocaridid genus *Mirocaris* by having dorsolateral spines on the telson arranged in sinuous rows, the possession of more than two rows of accessory spines on the ventral surfaces of the third to fifth pereopods and the absence of pereopodal epipods. The presence of a strong, sharp pterygostomian tooth also differentiates *Shinkaicaris* from *Chorocaris*, *Mirocaris*, and *Rimicaris*.

Shinkaicaris leurokolos (Kikuchi and Hashimoto, 2000), comb. nov.

(Figures 27, 28)

Alvinocaris brevitelsonis Kikuchi and Hashimoto 2000, p 141 (part), Figure 3i.

Alvinocaris leurokolos Kikuchi and Hashimoto 2000, p 141, Figures 4–7 [type locality: Depression C, Minami-Ensei Knoll, Mid-Okinawa Trough, 28°23.35'N, 127°38.38'E, 705 m].

## Material examined

Okinawa Trough. DS *Shinkai* 2000: dive 549, Depression C, Minami-Ensei Knoll, 28°23.35'N, 127°38.38'E, 705 m, 3 June 1991, suction sampler, coll. J. Hashimoto, one ovigerous female CL 12.5 mm (holotype; NSMT-Cr 12457); two males CL 10.5, 11.5 mm, two females CL 9.2, 9.9 mm (paratypes; NSMT-Cr 12459).

## Description

Integument of body thin, but not membranous, surface shining.

Rostrum (Figure 27A, B) compressed laterally, reaching distal margin of first segment to midlength of second segment of antennular peduncle; dorsal margin armed with 7–10 teeth slightly diminishing in size anteriorly, including six to nine on rostrum proper and one to three on carapace, posteriormost tooth arising from level of posterior margin of orbit to 0.08 of carapace length; lateral carina sharp, broadened proximally and confluent with orbital margin; ventral surface bluntly carinate medially, unarmed. Carapace (Figure 27A, B) somewhat compressed laterally; postrostral median ridge relatively low, rather blunt, extending to 0.40 length of carapace; antennal tooth sharp, distinctly buttressed, margin inferior to antennal tooth forming small rounded lobe (Figure 27C); pterygostomian tooth much larger than antennal tooth, strongly produced anteriorly; lateral surface of carapace with shallow post-antennal groove originating inferior to base of antennal tooth, passing obliquely ventrad and extending to hepatic region. Strong median sternal spine between coxae of fifth pereopods.

Abdomen (cf. Figure 27D) smooth dorsally; pleural margin of anterior two somites broadly rounded, that of third somite broadly rounded or with one small posteroventral tooth; pleuron of fourth somite with acute posterolateral tooth and occasionally with additional one to three acute teeth on posterior margin; pleuron of fifth somite with two to four posterior teeth including posteroventral tooth. Sixth somite 1.20–1.30 times as long as proximal height, with sharp posterolateral process and posteroventral tooth. Telson (Figure 27E) elongate subrectangular, length 2.50–2.90 times anterior width, 2.90–3.20 times posterior width, with five to seven dorsolateral spines arranged in a sinuous row;



Figure 27. *Shinkaicaris leurokolos* (Kikuchi and Hashimoto, 2000), comb. nov. (A) Carapace and cephalic appendages, lateral; (B) anterior part of carapace and cephalic appendages, dorsal; (C) eye, left orbit and antennal tooth, dorsal; (D) third to sixth abdominal somites, lateral; (E) telson and right uropod, dorsal (marginal setae on uropod omitted); (F) posterior margin of telson, dorsal. Paratype female from Minami-Ensei Knoll, Mid-Okinawa Trough (CL 11.6 mm; NSMT-Cr 12459).



Figure 28. *Shinkaicaris leurokolos* (Kikuchi and Hashimoto, 2000), comb. nov. (A) Left antennal scale, dorsal (marginal setae omitted); (B) left third maxilliped, lateral; (C) antepenultimate segment (merus-ischium-basis fused segment) of left third maxilliped, mesial; (D) coxa, epipod and basal part of antepenultimate segment of left third maxilliped, dorsal; (E) left first percopod, lateral; (F) chela of left first percopod, outer; (G) left third percopod, lateral; (I) same, ventral. Holotype female from Minami-Ensei Knoll, Mid-Okinawa Trough (CL 11.6 mm; NSMT-Cr 12457).

posterior margin convex, with two pairs of lateral spines (mesial pair longer than lateral) and 22–24 long plumose setae (Figure 27F).

Eyes (Figure 27A–C) on basally separated, movable stalks broadly fused mesially; division of corneal region and stalk unclear; corneal region, unfaceted, with irregular, scattered pigment-like masses within stalk; anteromedial face flat, sloping to anterolateral face, without spiniform tubercle on anterior surface.

Antennular peduncle (Figure 27A, B) moderately stout. First segment with conspicuous fossa on dorsal surface subproximally, and with conspicuous distolateral tooth; stylocerite slender, reaching midlength to distal margin of second segment, slightly depressed dorsoventrally, sharp, separated from first segment by narrow, deep incision and succeeding deep groove; dorsal surface of stylocerite with distinct rounded tubercle subproximally and transverse row of setae somewhat distal to subproximal tubercle. Second segment 1.30–1.50 times as long as wide, with distomesial tooth. Third segment short. Dorsolateral flagellum longer than carapace, thickened aesthetasc-bearing portion in basal 0.40–0.50, ventromesial flagellum somewhat longer.

Antenna (Figure 27A, B) with stout basicerite bearing ventrolateral distal spine and ventrodistal spine. Antennal scale (Figure 28A) 0.48–0.52 times as long as carapace, 1.70–2.00 times as long as wide; lateral margin straight or slightly convex, strongly converging against dorsal median ridge; distolateral tooth broad, directed forward, falling short of broadly rounded distal margin of blade, mesial margin slightly curved or straight. Carpocerite moderately stout. Antennal flagellum longer than body.

Mouthparts similar to those of *Alvinocaris* (illustrated by Kikuchi and Hashimoto 2000). Third maxilliped (Figure 28B, C) slender, composed of four segments, reaching beyond distal end of antennal scale by half length of ultimate segment; distal two segments slightly arched in lateral view; ultimate segment trigonal in cross-section, tapered distally, bearing terminal cluster of five to seven small spines, row of sparse long spiniform setae on dorsomesial, dorsolateral and ventral margins, and transverse tracts of dense setae along mesial face; carpus (penultimate segment) shorter than ultimate segment, also with transverse tracts of setae on mesial face; antepenultimate (merus-ischium-basis fused segment) subequal to distal two segments combined, somewhat sinuously curved in dorsal view, distal half weakly compressed laterally and proximal half somewhat flattened dorsoventrally, with slender spine at distolateral ventral corner, margins with short to long setae; mesial face with some short oblique rows of spiniform setae distal to midlength of segment; tufts of long setae at proximomesial portion of antepenultimate segment; coxa with epipod rather abruptly tapering distally (Figure 27D); exopod absent.

First percopod (Figure 28E) falling short of tip of third maxilliped, moderately robust, not strongly polymorphic. Fingers curved downward and inward; dactylus more than three times longer than palm; outer surface of both fingers convex, inner concavity with opposed edges uniformly offset, closing without gape, each armed with fine row of almost uniform, erect, corneous teeth so closely set as to be contiguous, tip of each finger slightly spooned; submarginal row of tufts of short sensory setae on inner surface along cutting edges. Palm extremely short, inflated (Figure 28F). Carpus cupped distally to receive palm; dorsodistal margin not produced; ventral surface flared into weak lateral ridge terminating in small tooth and smaller mesial ridge ending bluntly, surface between ridges with thick grooming setae and one or two movable spines; mesial face with shallow depression. Merus and ischium obliquely articulated in lateral view; merus not inflated ventrally, without small subdistal tooth on ventrolateral margin; ischium always unarmed.

Second percopod subequal in length to, but more slender than first percopod, not reaching distal margin of antennal scale. Fingers subequal in length to palm, each terminating in small, corneous unguis crossing each other when closed, cutting edges without gape, each pectinate with single row of minute teeth directed obliquely distally and increasing slightly in size. Carpus slightly longer than chela. Merus and ischium obliquely articulated in lateral view; ischium unarmed.

Third to fifth percopods (cf. Figure 28G) moderately slender, generally similar in length and structure, third reaching beyond distal margin of antennal scale by 0.30–0.40 length of propodus. Propodus–carpus combined shorter than merus–ischium combined in third, subequal in fourth, and longer than in fifth. Dactyli (cf. Figure 28H, I) short, 0.18–0.22 times as long as propodi, terminating in strong unguis, armed with 13–16 accessory spines arranged in three or four rows on flexor surface; accessory spines grading from small proximally to longest and strongest distally. Propodi of third and fourth percopods with slender spinules arranged in two rows on ventral surface; propodus of fifth percopod with numerous spiniform setulose setae arranged in three or four rows on distal half of ventral surface. Carpi distinctly shorter than propodi. Meri and ischia unarmed.

First to fourth percopods each without pre-coxal spine.

Pleopods well developed. First pleopod with endopod 0.50–0.60 length of exopod, sexually dimorphic; in males, distal part abruptly narrowed, bearing four to six curved spiniform setae; in females, distal part gradually tapered, with fringe of plumose setae similar to those fringing remaining margins. Second to fifth pleopods with endopods slightly shorter than exopods; appendices internae on second to fourth pleopods not greatly reduced in size, but slender, simple; appendix interna on fifth pleopod more stout than others, with distomesial cluster of cincinnuli. Appendix masculina robust, slightly shorter than appendix interna, with several (up to eight) terminal and subterminal spines.

Uropod (Figure 27E) with rami subequal in length, exopod with small movable spine mesial to smaller distolateral tooth and sinuous diaeresis (not depicted on Figure 27E).

#### Distribution and habitat

Known only from Minami-Ensei Knoll, Mid-Okinawa Trough, at a depth of 705 m. This species occurs in a thermally influenced area.

#### Variation

Variation in the rostral shape and armature was fully illustrated by Kikuchi and Hashimoto (2000, Figure 7a–j). It is noteworthy that this species does not show strong polymorphism in the morphology of the first percopod.

#### Biogeography

Species of Alvinocaris and Shinkaicaris leurokolos are restricted to chemosynthetic environments. Six species of Alvinocaris (A. brevitelsonis, A. dissimilis sp. nov., A. longirostris, A. lusca, A. markensis, and A. williamsi) and the sole species of Shinkaicaris (S. leurokolos comb. nov.) are known from hydrothermal vents (Williams and Chace 1982; Williams 1988; Kikuchi and Ohta 1995; Shank et al. 1999; Kikuchi and Hashimoto 2000; Ohta and Kim 2001; Shank and Martin 2003), while A. muricola and A. stactophila appear to be endemic to cold seeps (Williams 1988; present study).

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Information on the geographic and bathymetric distributions of *Alvinocaris* is still limited or incomplete, considering the rather few areas explored at present (about 15 sites have been described in detail; see Sibuet and Olu 1998). Therefore, it is difficult to discuss satisfactorily the biogeography of species of *Alvinocaris*. Information on geographical distribution, bathymetric range and types of habitat derived from the available data is summarized in Table III and Figure 29. It is apparent that the geographical range of each species is rather limited, although the genus is widely distributed in the Atlantic (four

Species	Locality	Depth (m)	Type of habitat
A. lusca	East Pacific Ridge (between 0° and 13°N)	2400-2600	Hydrothermal vents
A. longirostris	Okinawa Trough (Iheya Ridge, Hatoma Knoll)	1053-1627	Hydrothermal vents
	Sagami Bay (Off Hatsushima site)	1120-1220	Cold seeps
A. brevitelsonis	Okinawa Trough (Minami-Ensei Knoll)	705	Hydrothermal vents
A. dissimilis sp. nov.	Okinawa Trough (Minami-Ensei Knoll)	705	Hydrothermal vents
A. markensis	Mid-Atlantic Ridge (Lucky Strike to	1693-3650	Hydrothermal vents
	Logatchev)		
A. williamsi	Mid-Atlantic Ridge (Menez Gwen)	845-865	Hydrothermal vents
A. muricola	Florida Escarpment, Gulf of Mexico	3277	Cold seeps
	South Barbados	1697	Cold seeps
	Congo Basin	3110-3155	Cold seeps
A. stactophila	Central Gulf of Mexico	534	Cold seeps
Indeterminate species			
Alvinocaris sp. 1	Central Gulf of Mexico	534	Cold seeps
Alvinocaris sp. 2	Edison Seamount, western Pacific	1483	Hydrothermal vents
Alvinocaris spp. 3, 4	Bay of Plenty, New Zealand	Unreported	Hydrothermal vents
Alvinocaris sp. 5	Blake Ridge, north-western Atlantic	2155	Cold seeps

Table III. Summary of geographic distribution, bathymetric range and general habitat of Alvinocaris species



Figure 29. Distribution map of Alvinocaris species known at present.

described and two undescribed species) and the Pacific (four described and at least four undescribed species). Species endemic to cold seeps are so far known with certainty only from the Atlantic Ocean, although the north-western Pacific A. longirostris occurs in both hot vents and cold seeps (see "Remarks" for A. longirostris). No representative of Alvinocaris has been reported from the Indian Ocean, although two alvinocaridid species, Rimicaris kairei Watabe and Hashimoto, 2002, and an indeterminate species of Chorocaris, were recently discovered from the active hydrothermal vents on the Central Indian Ridge (Van Dover et al. 2001; Watabe and Hashimoto 2002). As mentioned before, A. lusca is known with certainty only from the Galapagos Rift (2450 m) and in the northern East Pacific Rise at 9°N (2520 m) (Shank et al. 1999). Alvinocaris markensis and A. williamsi are reported from the Mid-Atlantic Ridge. It is noteworthy that A. markensis shows rather wide geographical and bathymetric ranges (Lucky Strike, Rainbow, Broken Spur, TAG, and Logatchev, at depths ranging from 1693 to 3650 m; Shank et al. 1999; present study), while A. williamsi is so far restricted to Menez Gwen (845-866 m) (Shank and Martin 2003; present study). Alvinocaris stactophila and Alvinocaris sp. 1 are known only from the Louisiana Escarpment in the Gulf of Mexico (534 m), representing the certain shallowest record for the genus. It is remarkable that three congeneric species, A. longirostris, A. brevitelsonis, and A. dissimilis sp. nov., occur within a small area in the Okinawa Trough in the north-western Pacific. Alvinocaris longirostris is so far known only from the southern part of the Okinawa Trough, i.e. Iheya Ridge and Hatoma Knoll, at depths of 1053-1627 m and from Off Hatsushima site, Sagami Bay, at depths of 1120-1220 m, while A. brevitelsonis and A. dissimilis are both recorded from the same location on the Minami-Ensei Knoll, in the northern part of the Okinawa Trough, at a depth of 705 m, where Shinkaicaris leurokolos co-occurs. It is probable that A. longirostris and the other two Alvinocaris species are bathymetrically separated, as sympatric occurrence of the three species has not been recorded despite their geographical proximity.

Most remarkable is that populations of A. muricola occur in both the western and eastern Atlantic (Florida Escarpment, Gulf of Mexico, 3277 m; Barbados, SE Caribbean, 1697 m; and Gulf of Guinea, 3110-3155 m), separated by the Mid-Atlantic Ridge. The distance between the West Florida Escarpment and the Congo Basin is about 9000 km, quite exceptionally great compared to the limited geographical range of other congeneric species. In spite of a different geological context, however, these areas have in common discharges of fluids rich in methane and other reduced compounds. These conditions may support the development of bacterial populations that sustain similar animal communities. In fact, some of the faunal elements are possibly closely related between the western and eastern Atlantic. For example, the unidentified mytilid bivalve of the genus Bathymodiolus from the Congo Basin is closely related to B. heckerae Turner, Gustafson, Lutz and Vrijenhoek, 1998, known from the Florida Escarpment and Blake Ridge, and B. boomerang Cosel and Olu, 1998 from Barbados (R. von Cosel, personal communication). Two populations of vestimentiferan worm from the Florida Escarpment and the west equatorial African margin may belong to the same species, *Escarpia* n. sp. (Andersen et al. 2004). The presence of common or phylogenetically close species in the seep communities between the Gulf of Mexico and the Gulf of Guinea may be explained by the existence of a longitudinal flow and movement of North Atlantic deep water through fracture zones near the equator and at 23°S, which may provide faunal linkages between these communities (Van Dover et al. 2002). Furthermore, amphi-Atlantic distribution is shown by a number of deep-water decapod taxa, such as nematocarcinids (Crosnier and Forest 1973), bathypalaemonellids (Crosnier and Forest 1973; Cleva 2001), glyphocrangonids (Holthuis 1971), crangonids

(Gore 1985; d'Udekem d'Acoz 1999) and parapagurids (Lemaitre 1989). However, it is still difficult to explain satisfactorily the process of transportation of larvae of A. muricola for such great distance, as the species appears to depend on seep habitats. As mentioned before, there is no evidence to support the presence of A. muricola in hydrothermal vents on the Mid-Atlantic Ridge. If our decision that the two separate populations of Alvinocaris shrimp belong to the same species is correct, it is suggested that suitable habitats (cold seeps) may be present in the intervening area.

The other locations where *Alvinocaris* species occur include hydrothermal vents on the Edison Seamount and North Fiji Basin in the western Pacific (Shank et al. 1999; K. Baba, personal communication; this study), vents on the Brothers and Rumble calderas, north of New Zealand, south Pacific (W. R. Webber, personal communication) and cold seeps on the Blake Ridge in the north-western Atlantic (Van Dover et al. 2003) (Table III; Figure 29). Future investigations will eventually reveal the existence of more unknown species either from known or as yet undiscovered chemosynthetic localities.

The most striking feature of the phylogeny of the Alvinocarididae proposed by Shank et al. (1999; as Bresiliidae) is that the species of *Alvinocaris* did not cluster according to biogeographic regions. Our morphological comparison agrees with this hypothesis. For example, the two species known from the Mid-Atlantic Ridge, *A. markensis* and *A. williamsi*, are not closely related. *Alvinocaris markensis* is very similar to *A. longirostris* and *A. muricola*, while *A. williamsi* is rather distinctive within the genus. The two sympatric species, *A. brevitelsonis* and *A. dissimilis* sp. nov., are not most closely related. *Alvinocaris brevitelsonis* is rather similar to *A. lusca*, and *A. dissimilis* sp. nov. resembles *A. longirostris*, *A. markensis*, and *A. muricola*. These may suggest that geographical isolation contributed to early stages of speciation of species of *Alvinocaris*, and the current colonization was established after speciation.

Abundance of individuals of Alvinocaris species is distinctly higher in seep habitats than in hot vents. For example, more than 300 individuals per  $m^2$  of A. muricola over mussel beds was recorded at the Régab site (west equatorial African margin) and at shallow mud volcanoes of south Barbados (tropical western Atlantic), whereas the density of vent species, such as A. markensis and A. longirostris, is low (personal observation; Watabe and Miyake 2000) and isolated. The difference in abundance between seep and vent species is probably the consequence of a higher rate of trophic resources available for shrimp in the cold seeps than in hot vents.

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## Note added to proof

After the revised manuscript of this paper was submitted to the editor, a paper reporting two species of *Alvinocaris* from hydrothermal vents north of New Zealand, *A. niwa* Webber, 2004, and *A. longirostris* Kikuchi and Ohta, 1995, has been published (Webber 2004). According to Webber's (2004) original description, *A. niwa* has two rows of spines on the ventral (flexor) surfaces of the dactyli of the third to fifth pereopods, a character that sets apart *A. niwa* from *Alvinocaris*, as discussed in this paper. As Webber (2004) clealy stated, *A. niwa* appears similar to *Shinkaicaris leurokolos*. Further study is needed to determine the generic position of *A. niwa*. The geographical range of *A. longirostris* is now greatly extended to the South Pacific.

#### Reference

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