A new caridean shrimp of the family Alvinocarididae from thermal vents at Menez Gwen on the Mid-Atlantic Ridge

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Abstract.—A new species of alvinocaridid shrimp, *Alvinocaris williamsi,* is described from the Menez Gwen hydrothermal vent field on the Mid-Atlantic Ridge. The new species is most similar to another relatively shallow water alvinocaridid, *A. stactophila* Williams, known only from a cold seep area off the coast of Louisiana, but differs in details of the rostrum and appendages. *Alvinocaris williamsi* is also morphologically similar to two species of the genus recently described from the Mid-Okinawa Trough, Japan. Molecular phylogenetic studies of *A. williamsi,* the eighth described member of the genus, may provide significant insights into the role that deep-sea hydrothermal vents at mid-ocean ridges and hydrocarbon seeps on continental margins have played in the evolution of fauna endemic to these chemosynthetic habitats.

The caridean shrimp family Alvinocarididae was originally proposed by Christoffersen (1986) to accommodate a number of morphologically similar shrimp known from hydrothermal vents and hydrocarbon seeps. The family was further diagnosed by Segonzac et al. (1993) in a footnote, and also by Vereshchaka (1996a, 1996b, 1997) (see Martin & Davis 2001). To date, five genera have been proposed for the family. In the order in which they were proposed, they are: *Alvinocaris* Williams & Chace, 1982; *Rimicaris* Williams & Rona, 1986; *Chorocaris* Martin & Hessler, 1990; *Opaepele* Williams & Dobbs, 1995; and *Iorania* Vereshchaka, 1996b (see Shank et al. 1998 for the synonymy of *Iorania* and *Rimicaris*). A sixth genus of vent shrimp, *Mirocaris* Vereshchaka, 1997, was proposed by Vereshchaka (1997) for *Chorocaris fortunata* Martin & Christiansen (1995) and for a new species (*M. keldyshi* Vereshchaka, 1997); however, this genus was transferred to the newly created family Mirocarididae by Vereshchaka (1997).

The type genus of the Alvinocarididae, *Alvinocaris,* is the most diverse genus of the family and contains five hydrothermal vent-endemic species: *A. brevitelsonis* Kikuchi & Hashimoto, 2000, from the Minami-Ensei Knoll in the Mid-Okinawa Trough off Japan; *A. leurokolos* Kikuchi & Hashimoto, 2000, also from the Minami-Ensei Knoll; *A. longirostris* Kikuchi & Ohta, 1995, from the Iheya Ridge off Japan; *A. lusca* Williams & Chace, 1982, from the Galapagos Rift in the eastern Pacific; and *A. markensis* Williams, 1988, from the Mid-Atlantic Ridge. Another two species of *Alvinocaris* are endemic to chemosynthetic habitats associated with hydrocarbon and brine seeps: *A. muricola* Williams, 1988, from the West Florida Escarpment; and *A. stactophila* Williams, 1988, from the Louisiana Slope in the northern Gulf of Mexico. The study of additional collections, including undescribed hydrothermal-associated shrimp specimens from the Edison Seamount of the Bismark Archipelago in Papua New Guinea (Shank et al. 1999; K. Baba, pers. comm.),

from the Logatchev vent field of the Mid-Atlantic Ridge (A. Vereshchaka, pers. comm.), and several recently recovered from active seamounts north of the Bay of Plenty (northern North Island, New Zealand) (Rick Webber and Neil Bruce, pers. comm., http://www.niwa.co.nz/pubs/bu/05/blind) may yield additional new species of *Alvinocaris*. The pan-equatorial biogeographic distribution of the genus is noteworthy. *Alvinocaris* species occur in almost every biogeographic vent province (except the Northeast Pacific vents; Shank et al. 1999). However, recent initial investigations of hydrothermal vents in the Indian Ocean did not reveal the presence of *Alvinocaris* shrimp despite the common appearance of the other dominant Atlantic and Pacific genera *Rimicaris* and *Chorocaris* (Hashimoto et al. 2001, Van Dover et al. 2001). The *Alvinocaris* species described herein occupies the northernmost extent of the generic range, as it inhabits the Menez Gwen vent site, the most shallow vent field (850 m) and the most northern known active deep-sea hydrothermal site along the Mid-Atlantic Ridge (37°50.5′N, 31°31.3′W) (Gebruk et al. 1997, Colaço et al. 1998, Comtet & Desbruyères 1998, Desbruyères et al. 2001). Below, we describe a new species of *Alvinocaris* from the Menez Gwen hydrothermal vent field, and suggest evolutionary relationships with other alvinocarid species.

Materials and Methods

All specimens were collected using the human occupied submersible *DSV Alvin* at the Menez Gwen hydrothermal vent field, northern Atlantic Ocean. Shrimp were collected from a cluster of active individuals among clumps of mussels, *Bathymodiolus azoricus* Von Cosel, Comtet & Krylova, within vent flow with a 30 cm × 30 cm square "black net" (BN) operated using the manipulator arm by the pilots of *DSV Alvin*. A total of 14 specimens were collected (from a single net sample) from areas of most intense diffuse fluid within the central portion of a hydrothermally-active mussel bed community that included a more abundant alvinocaridid species, *Mirocaris keldyshi*, amphipods, *Luckia striki* Bellan-Santini & Thurston, gastropods, e.g., *Lepetodrilus* spp. and *Protolira valvatoides* Waren & Bouchet, polychaetes, e.g., *Branchipolynoe seepensis* Pettibone, and crabs, *Segonzacia mesatlantica* (Williams, 1988) and *Chaceon affinis* (A. Milne-Edwards & Bouvier, 1894). Specimens were brought to the surface in an insulated container and placed in chilled water on-board ship. Whole shrimp were sorted by morphotype and either preserved in 4% buffered formalin in seawater and subsequently transferred to 70% ethanol or frozen at −70°C and subsequently transported on dry ice and stored at −80°C. Carapace length (CL) of each individual was measured in millimeters (mm) from the orbital margin to the posteriomedial margin of the carapace. We recognize that the description of new species within this family from relatively few individuals can be risky (see Shank et al. 1998); however, preliminary results of mitochondrial DNA sequence data (Shank, pers. obs.) complement morphological evidence that distinction of this species from other *Alvinocaris* species is warranted. The holotype and paratypes are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The remaining specimens are cryo-preserved at the Woods Hole Oceanographic Institution for ongoing molecular phylogenetic investigations by TMS.

Alvinocaris williamsi, new species
Figs. 1–3

Material examined.—14 females CL: 8.2, 8.2, 8.5, 8.7, 8.9, 8.9, 9.3, 9.5, 9.5, 9.5, 9.6, 9.6, 9.7, 10.1, *DSV Alvin,* Dive 3117, Menez Gwen hydrothermal vent field, North Atlantic Ocean, 37°50.5′N, 31°31.3′W, 850 m, 7 Jul 1997.
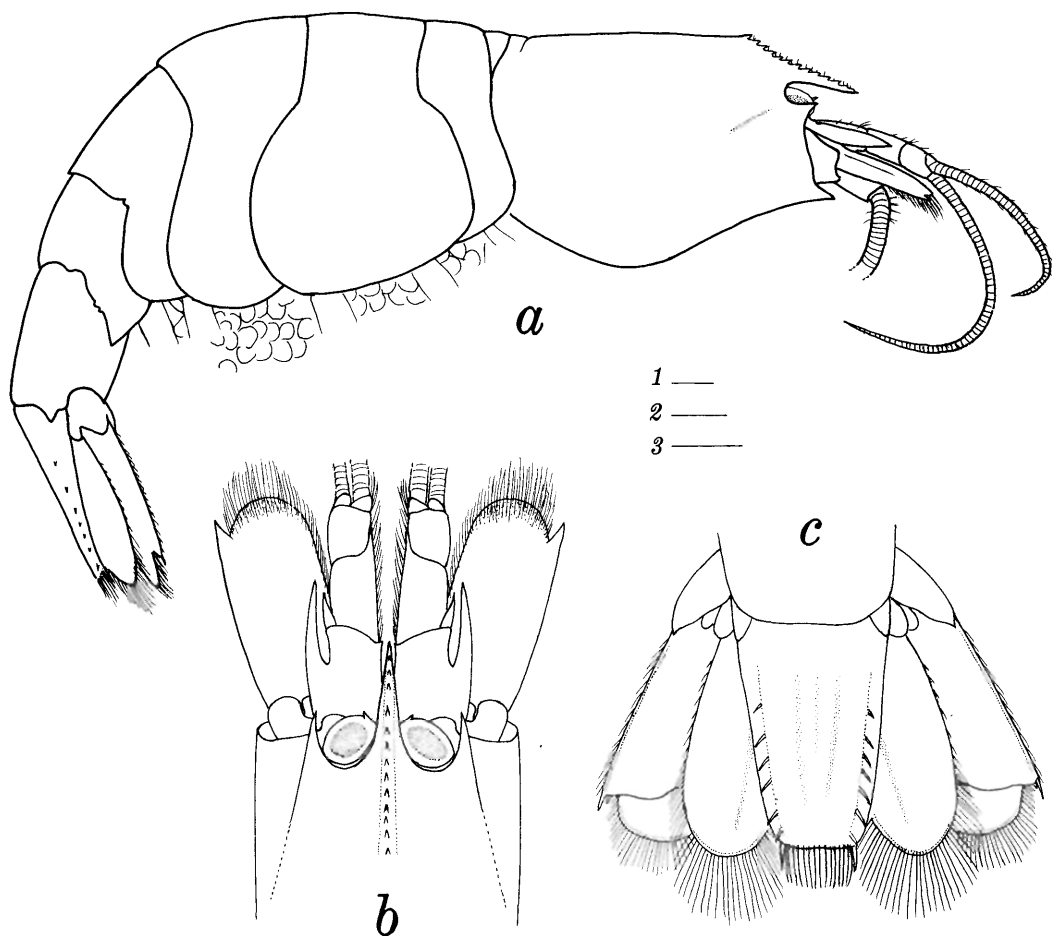
Types.—All from *DSV Alvin* Dive 3117.

Fig. 1. *Alvinocaris williamsi,* new species, holotype ovigerous female, USNM 1009651. *a,* body, cephalic appendages, and abdomen, lateral view; *b,* anterior region of carapace, including eyes and antennae, dorsal view; *c,* telson and uropods, dorsal view. Scale bars equal 1.0 mm (bar 1 for *a,* bar 2 for *b,* bar 3 for *c*).

Holotype: adult female CL 9.5 mm, ovigerous (specimen ID: BN 70), USNM 1009651. Paratypes: 2 adult females CL 9.3, 9.7 (specimen ID: BN 68 and BN 51, respectively), abdomen torn from body, tail fan missing, USNM 1009652, USNM 1009653.

Description.—Integument thin, shining, minutely punctuate. Rostrum (Fig. 1a, b) almost straight, imperceptibly elevated above horizontal in distal half; sharply pointed tip (broken or slightly blunted in all specimens) reaching at least to level of articulation between first and second peduncular segment of second antenna or sometimes to midlength of second segment; dorsal margin raised into thin serrate crest containing 13 or 14 teeth of nearly equal strength in central sector of row, about 0.5 length of crest continued onto carapace, deflecting from dorsal line of carapace at approximate 45° angle; ventral margin less prominent, straight, and unarmed or with 1 minute subterminal tooth; lateral carina (not visible in Fig. 1a) broadened proximally and confluent with orbital margin. Carapace (Fig. 1a) with buttressed and distinct antennal spine; pterygostomian spine prominent, acuminate. Anterior antennal carina curving posteroventrally from near base of antennal

spine to intersect at about midlength of carapace with carina extending posteriorly from pterygostomial spine, its associated groove (not visible in Fig. 1b) continuing indistinctly posteriorly.

Abdomen of female broadly arched dorsally, gradually tapering posteriorly, height of sixth somite about half that of first somite. Pleura of third somite broadly rounded, that of fourth somite irregularly rounded, flanked dorsally by single remote obsolescent spine; fifth pleuron with strong acute triangular posteroventral tooth flanked dorsally by cluster of 2 or 3 remote small spines on margin; sixth somite with middorsal length about 1.4–1.9 that of fifth somite, broad-based posterolateral tooth overlapping base of telson, smaller posterolateral spine acute. Telson (Fig. 1c) elongate, subrectangular, length (not including posterior teeth) about 2.0–2.7 anterior width, 3.2–3.7 posterior width, about 1.3–1.5 length of sixth somite; armed with 5–7 dorsolateral spines of nearly uniform size, occasionally unequal in number on either side; posterior margin slightly convex, armed with 1 spine at each corner and 12 feathered strong setae on posterior margin between them.

Eyes (Fig. 1a, b) with cornea imperfectly developed; unfaceted though diffusely pigmented; ovate in outline though fused to each other mesially beneath rostrum, each with upturned spine on anterodorsal surface.

Antennular peduncle (Fig. 1b) extending slightly short of end of antennal scale; basal segment 2.1 length of second segment and about 2.2–2.5 length of third, all measured on dorsal margin; stylocerite well separated from peduncle, tapering to slender elongate tip variably reaching as far as midlength of second segment; basal segment with distodorsal margin exceeded by rostral tip though extended laterally into strong lateral spine reaching level nearly equal to that of stylocerite and closely appressed to second segment, much smaller distomesial spine slightly divergent; shorter second segment

with stronger mesiodistal spine. Antennal scale (scaphocerite) broadly rounded distally, with broad triangular tooth on distolateral border extending to same level as rounded distal border.

Mouthparts (Fig. 2) fairly typical for the genus. Mandible (Fig. 2a, b) with 6 blunt, uneven, terminal teeth plus one slightly sharper dorsal subterminal tooth along cutting border, and with long, blunt, posterior tooth ("molar process" of some authors) separated from cutting edge by a wide gap; mandible deeply excavate on internal (posterior) surface just above this blunt posterior tooth; mandibular palp 2-segmented, distal article bearing numerous plumose setae; basal article with 2 plumose setae on distal border. First maxilla (Fig. 2c) with 2 endites; coxal (distalmost) endite with row of evenly spaced and evenly sized blunt spines (arrow) in addition to dense plumose and simple setae; basial endite (proximal endite) with longer, curved setae but lacking spine row; palp unsegmented, with 2 short and 1 long terminal setae as illustrated. Second maxilla (Fig. 2d) scaphognathite with dorsal lobe broad, distally almost truncate, and lined with evenly spaced plumose setae; posterior lobe of scaphognathite tapering posteriorly, almost triangular, with setae increasing in length posteriorly, each seta angled and minutely serrate (for grooming); coxal lobe simple, blunt, setose; basial endite bilobed, each lobe fringed with plumose setae; palp thin, narrow, strap-like. First maxilliped (Fig. 2e) phyllopodous; coxal endite distally blunt and slightly recurved; basial endite bilobed, with distal lobe approximately twice length of proximal lobe; palp thin, tapering to acute distal tip bearing short setae and visible only in posterior view; exopod broad, expanded and rounded distally, lined on either side with evenly spaced plumose setae; epipod bilobed at base, fused distally, with dorsolateral lobe bearing weak posterior projection. Second maxilliped (Fig. 2f) pediform, 6-segmented; coxa expanded and rounded on medial surface, which bears nu-
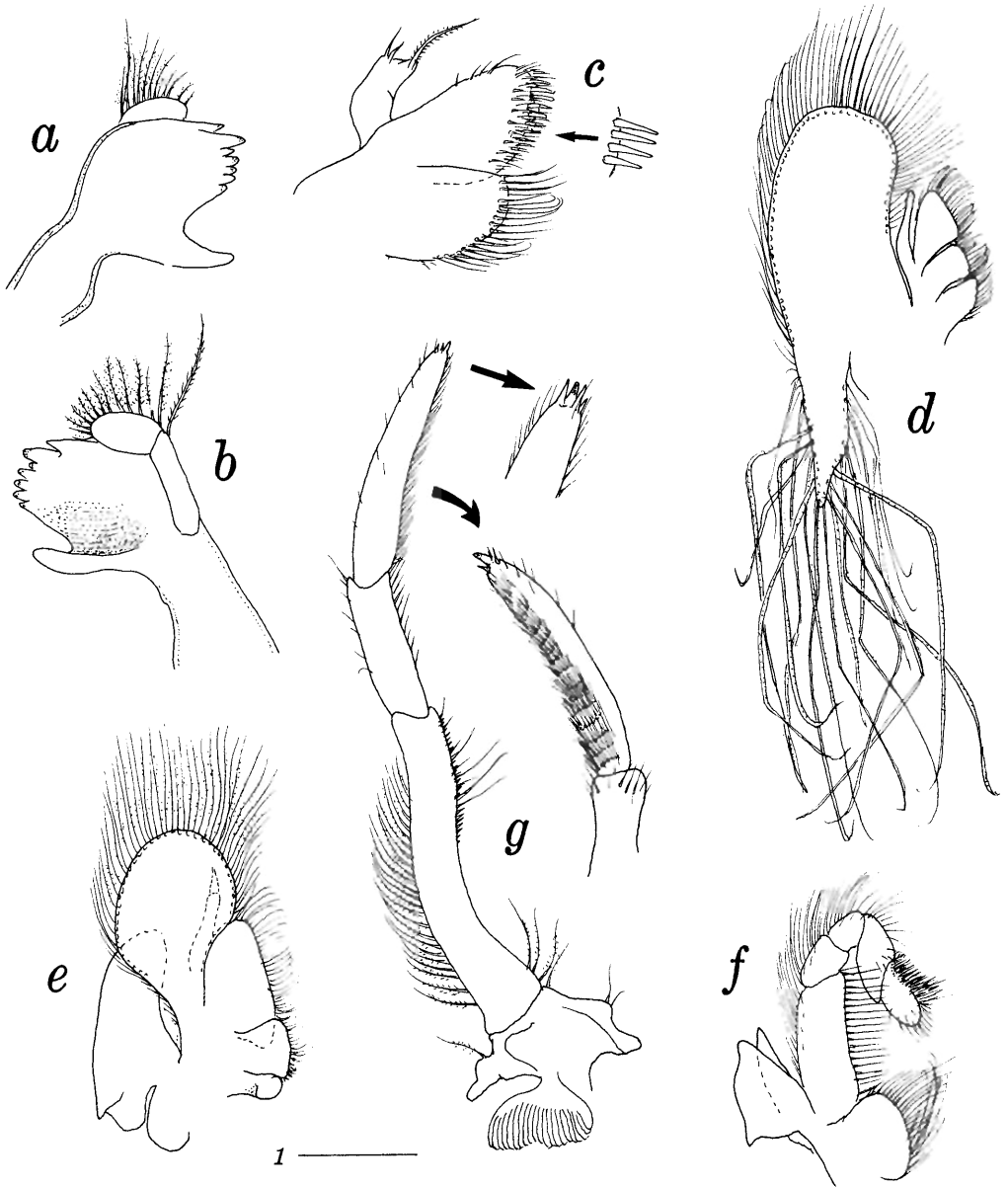
Fig. 2. *Alvinocaris williamsi,* new species, paratype female, USNM 1009653. Mouthparts, right side. *a,* mandible, outer (external) view; *b,* mandible and palp, inner view; *c,* first maxilla, with row of evenly spaced spines magnified and indicated by arrow; *d,* second maxilla; *e,* first maxilliped; *f,* second maxilliped; *g,* third maxilliped, with tip enlarged (upper arrow) and inner surface with rows of setae displayed (lower arrow). Scale bar 1 equals 0.5 mm (*a, b, c*), and 1.0 mm (*d, e, f, g*).

merous plumose setae; fused basi-ischium with evenly spaced plumose setae along medial border; merus and carpus short; propodus trapezoidal; dactylus short, distally rounded, with brush like patch of dense se-

tae on proximal region. Epipod nearly triangular, with weak lobe coming off posterior surface. Third maxilliped (Fig. 2g) pediform, elongate, 4-segmented; coxal segment short, with minute epipod bearing 1

or 2 setae; distal 3 segments elongate and pediform; basal of these with plumose setae on proximal medial border and row of plumose setae along dorsolateral border; dactylus tipped with acute sclerotized spines surrounding central claw-like tip (arrow), and with evenly spaced densely packed rows of stiff, minutely serrulate setae on ventro-medial surface (curved arrow).

First pereopods (Fig. 3a, b) chelate, subequal; fingers curved ventrally and slightly laterally; dactylus more slender than fixed finger, tips varying slightly in relative length, mesial surface of each finger concave; cutting margins uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory setae
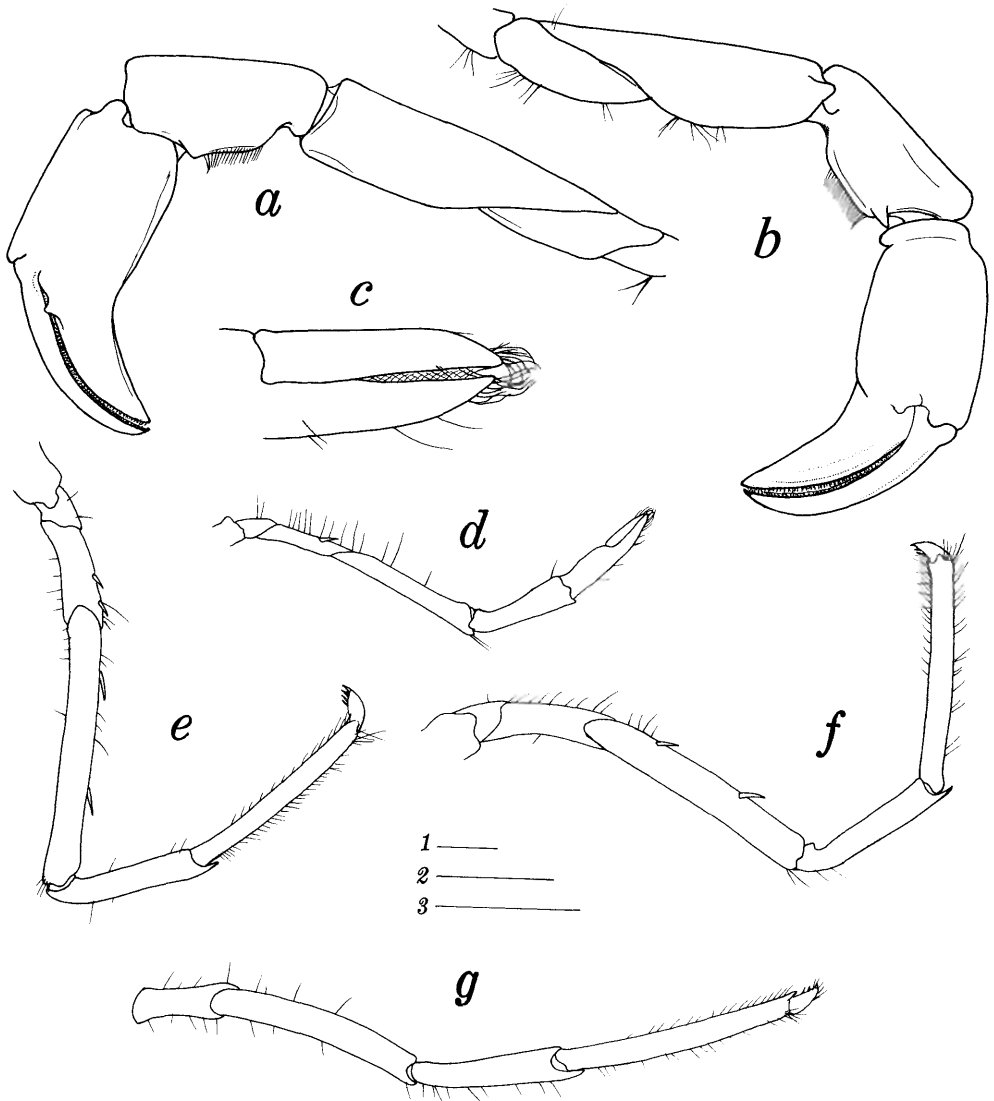

Fig. 3. *Alvinocaris williamsi,* new species, paratype female, USNM 1009652. *a,* right first pereopod (cheliped), inner view; *b,* right first pereopod, outer view; *c,* left second pereopod, tip of chela; *d,* left second pereopod; *e,* left third pereopod; *f,* left fourth pereopod; *g,* left fifth pereopod. Scale bars 1 and 2 equal 1.0 mm; scale bar 3 equals 0.5 mm (bar 1 for *d, e, f, g*; bar 2 for *a, b*; bar 3 for *c*).

mesial to cutting edges, acute tip of dactylus slightly spooned by elongate teeth slanted posteriorly and curving around external edge; entire leg slightly shorter than third maxilliped. Palm inflated but not elongate, approximately equal in length to fingers. Carpus measured along dorsal border slightly longer than palm, bearing oblique ventral crest, ending in strong distolateral spine (Fig. 3b) and flanked mesially by patch of setae on polygonal raised area; notch above spine smoothly concave, opposing low ridge ending in small rounded spine on heel of palm; shallowly concave anteromesial margin of carpus leading dorsally to 2 low rounded lobes. Merus swollen in distal half, distinct from ischium but fused to it, neither armed.

Second pereopod (Fig. 3c, d) shorter and more slender than first, reaching to between midlength and end of antennal peduncle; finger slightly longer than palm, similar in size and shape, opposed margins without gape, each pectinate with single row of teeth in distal half directed obliquely distally and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.2 times longer than chela; merus unarmed, ischium with stout spine at approximately 0.75 length.

Third to fifth pereopods (Fig. 3e, f, g) similar in length and structure, third reaching beyond antennal scale by about 0.3 the length of the propodus. Segments of these pereopods composed of: short dactylus armed with about 6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; ventral row of spines on propodus leading to base of dactylus; carpus of each leg with distodorsal extension variously projecting as a stop along proximal part of propodal extensor surface; third leg with ischium and merus stronger than on fourth and fifth leg, merus of third with ventral spine at 0.3 and 0.6 length, distal spine tending to be strongest, and ischium with 2 spines in line with those on merus; fourth leg with similar spines on merus but ischium not always bearing spines; fifth leg without spines on merus or ischium but with ventral row of small spines on propodus preceding base of dactylus.

Pleopods (not illustrated) well developed, first pair with endopods about half length of exopods; endopods tapering to acute tip.

Uropods (Fig. 1c) with rami subequal in length, slightly exceeding posterior margin of telson; lateral ramus of exopod with movable spine mesial to larger distolateral tooth, diaeresis sinuous.

Etymology.—The species name commemorates the late Austin B. Williams, Research Scientist of the Systematics Laboratory and National Marine Fisheries Service at the National Museum of Natural History, Smithsonian Institution (see Lemaitre & Collette 2000). We are all beneficiaries of his ceaseless pursuit of excellence in his contribution to the taxonomy, systematics, biogeography, and evolution of various decapod groups, including vent shrimp and crab species.

Remarks.—*Alvinocaris williamsi* appears morphologically most similar to *A. stactophila,* another species from a relatively shallow site (530 m). However, *A. stactophila* is known only from a distant hydrocarbon seep site (as opposed to a hot vent) off the coast of Louisiana, northern Gulf of Mexico. Characters shared by the two species include a rostrum that is unarmed (or occasionally armed with a single tooth) on the ventral margin (a feature also shared with *A. brevitelsonis* and *A. leurokolos* from the western Pacific). The dorsal and ventral margins of the rostrum are heavily toothed in all other described *Alvinocaris* species. Additionally, both *A. williamsi* and *A. stactophila* have a relatively short rostrum that continues posteriorly as a toothed carina that meets the dorsum of the carapace at an angle; this angle is sharper in *A. williamsi* and *A. stactophila* than in any other species except for *A. longirostris,* the distinctive rostrum of which, because of its

length and armature, could not be confused with that of either *A. stactophila* or *A. williamsi*. However, *A. williamsi* can be easily separated from *A. stactophila* by the sharper angle of the rostrum and carina where they meet the dorsal line of the carapace (approximately 45° in *A. williamsi* vs. approximately 30° in *A. stactophila*), by the relative length and width of the telson (which is considerably longer and narrower in *A. stactophila*), and by the shorter rostrum relative to the carapace in *A. williamsi*.

Based on the absence of ventral teeth on the rostrum and the angle of the rostral carina and carapace, *A. williamsi* is also markedly similar to two species, *A. brevitelsonis* and *A. leurokolos* Kikuchi & Hashimoto (2000), recently described from the relatively shallow (~700 m) Mid-Okinawa Trough. However, Kikuchi & Hashimoto (2000) point out that there is significant variability in rostral characters, especially in *A. brevitelsonis* where the ventral rostral margin is usually toothed (there are seven spines on the ventral rostral margin of the holotype) but may be unarmed, especially in young individuals. *Alvinocaris leurokolos* lacks teeth on the ventral rostral margin, and is thus more similar to the new species *A. williamsi*. *Alvinocaris williamsi* is readily distinguishable from both of those species in having a lightly pigmented eye; the eye is unpigmented in both *A. brevitelsonis* and *A. leurokolos*.

The distribution of *Alvinocaris* species within the global biogeographic vent provinces is centered in lower-latitude regions (Shank et al. 1999), and the strong morphological similarities among extant *Alvinocaris* species living in relatively shallow water vent and seep environments (<800 m) in the Atlantic and Gulf of Mexico is striking. Gebruk (1997) and others have hypothesized that vent-endemic shrimp species are derived from shallow-water seep ancestors. A molecular phylogenetic approach to this hypothesis by Shank et al. (1999) suggested that the analyzed vent-endemic *Alvinocaris* (i.e., *A. markensis, A. lusca,* and unde-

scribed Edison Seamount specimens) were derived from the *A. stactophila* (seep) lineage. This suggests that the extant *Alvinocaris* lineages share a common seep ancestor. However, other vent-endemic lineages are basal to *Alvinocaris,* suggesting that vent lineages gave rise to a seep lineage that in turn gave rise to other extant vent lineages. Based on morphology, *A. williamsi* from the relatively shallow Menez Gwen site more closely resembles a seep-endemic species (i.e., *A. stactophila*) than other hot vent species, and therefore molecular genetic comparisons of *A. williamsi* with congeners from deep-sea hydrothermal vents, seamounts, back-arc basins, and hydrocarbon seeps would markedly improve our understanding of the evolution and radiation of these shrimp among diverse chemosynthetic environments throughout the world's oceans.

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