

A new species of the shrimp genus *Chorocaris* (Decapoda: Caridea: Alvinocarididae) from hydrothermal vents in the eastern Pacific Ocean

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Abstract.—*Chorocaris paulexa*, new species, the first member of the genus *Chorocaris* Martin & Hessler, 1990 reported from the eastern Pacific, is described based primarily on two specimens, one of which is ovigerous, collected by the DSV *Alvin* at the Homer hydrothermal (black smoker) vent site (17°S) on the southern East Pacific Rise (SEPR). Seven additional (non-type) specimens from other SEPR sites (Rapa Nui, Brandon vents) are also described and compared to the types. The new species is compared to its congeners *C. vandoverae* Martin & Hessler, 1990, from the Mariana Back-Arc Basin in the western Pacific, and *C. chacei* (Williams & Rona, 1986), from the Mid-Atlantic Ridge), as well as to *Mirocaris fortunata* (Martin & Christiansen, 1995) (Mid-Atlantic Ridge). The new species is markedly similar in morphology to both *Chorocaris vandoverae* and *C. chacei*, but it can be distinguished from either of those species by a combination of the relatively acute branchiostegal projection of the carapace border, extent of the rostrum, and shape of the antennal scale. The finding extends the known range of the genus *Chorocaris* ~11,000 km eastward (from the Mariana Back-Arc Basin) and stimulates evolutionary and biogeographic hypotheses to explain this Pacific-wide distribution of a shrimp genus specialized to inhabit hydrothermal vent systems.

To date, more than 125 species of decapod crustaceans representing 33 families have been reported from hydrothermal vents and cold seeps (Martin & Haney, in press). Shrimps in particular are now known from a substantial number of vents and seeps in the Atlantic and Pacific oceans (e.g., see Van Dover 1995; Vereshchaka 1996a, 1996b; Desbruyères & Segonzac 1997; Fowler & Tunnicliffe 1997; Gebruk et al. 1997; Shank et al. 1998; Shank & Martin 2003; Webber 2004) and are at times the dominant macrofaunal invertebrates at these sites, especially along the Mid-Atlantic Ridge and Indian Ocean vent sites. All endemic vent and seep shrimp, many of which were originally treated as

members of the Bresiliidae, are now treated as members of the family Alvinocarididae Christoffersen, 1986 (see Martin & Davis 2001, Komai & Segonzac 2003), a group that may have radiated to vent habitats during the Miocene (Shank et al. 1999). Currently described vent-endemic shrimp species belong to 5 genera (with the number of described species in parentheses): *Alvinocaris* (9), *Rimicaris* (2), *Chorocaris* (2), *Opaepele* (1), *Mirocaris* (1), and *Nautilocaris* (1) (see Table 1). Several more species are in various stages of being described (manuscripts in press or in preparation). Additionally, vagrant shrimp species (species not endemic to vents but found at or near them) include members of the families

Table 1.—Caridean shrimp species known from hydrothermal vents and cold seeps to date. See Martin and Haney (in press) for additional details and for information on numerous reports of shrimp (often to genus level only) from a wider variety of sites.

Species	Sites
Family Alvinocarididae	
<i>Alvinocaris brevitelsonis</i> Kikuchi & Hashimoto, 2000	OKT
<i>Alvinocaris leurokolos</i> Kikuchi & Hashimoto, 2000	OKT
<i>Alvinocaris longirostris</i> Kikuchi & Ohta, 1995	OKT, SB, NZ
<i>Alvinocaris lusca</i> Williams & Chace, 1982	EPR
<i>Alvinocaris markensis</i> Williams, 1988	MAR
<i>Alvinocaris muricola</i> Williams, 1988	WFE
<i>Alvinocaris niwa</i> Webber, 2004	NZ
<i>Alvinocaris stactophila</i> Williams, 1988	NGM
<i>Alvinocaris williamsi</i> Shank & Martin, 2003	MAR
<i>Chorocaris chacei</i> (Williams & Rona, 1986)	MAR
<i>Chorocaris paulexa</i> (this study)	SEPR
<i>Chorocaris vandoverae</i> Martin & Hessler, 1990	MARIANA
<i>Mirocaris fortunata</i> (Martin & Christiansen, 1995)	MAR
<i>Mirocaris</i> sp. (as <i>Chorocaris</i> sp. in Van Dover et al., 2001)	RTJ
<i>Nautilocaris saintlaurentae</i> Komai & Segonzac, 2004	NFB
<i>Opaepele loihi</i> Williams & Dobbs, 1995	LOIHI
<i>Rimicaris exoculata</i> Williams & Rona, 1986	MAR
<i>Rimicaris kairei</i> Watabe & Hashimoto, 2002	RTJ+
Family Oplophoridae	
<i>AcanthePHYra purpurea</i> Milne-Edwards, 1881	MAR
<i>AcanthePHYra eximia</i> Smith, 1884	KB
<i>Hymenodora glacialis</i> (Buchholz, 1874)	GAK
<i>Systellaspis braueri</i> Balss, 1914	EPR
Family Hippolytidae	
<i>Lebbeus carinatus</i> de Saint Laurent, 1984	EPR++
<i>Lebbeus washingtonianus</i> (Rathbun, 1902)	OKT
<i>Lebbeus bidentatus</i> Zarenkov, 1976	EPR*
Family Nematocarcinidae	
<i>Nematocarcinus productus</i> Bate, 1888	KB
<i>Nematocarcinus</i> sp.	EPR, JdF**
Family Pandalidae	
<i>Chlorotocus novaezealandiae</i> (Borradaile, 1916)	NZ
Family Palaemonidae	
<i>Pericilimenes thermohydrophilus</i> Hayashi and Ohtomi, 2001	KAG

Abbreviations for sites: EPR = East Pacific Rise; SEPR = Southern East Pacific Rise; GAK = Gakkel Ridge, Arctic Ocean; GAL = Galapagos; KAG = Kagoshima Bay, Japan; KB = Kanesu-no-se Bank, Enshu-nada, Japan; LOIHI = Loihi Seamount, Hawaii; MAR = Mid-Atlantic Ridge; MARIANA = Mariana Back-Arc Basin; NFB = North Fiji Basin (Komai & Segonzac 2004); NGM = Northern Gulf of Mexico; OKT = Okinawa Trough, Japan; RTJ = Rodriguez Triple Junction, Indian Ocean; SB = Sagami Bay, Central Japan (Fujikura et al. 1995); WFE = Western Florida Escarpment; NZ = New Zealand seamounts, Kermadec Ridge (*Alvinocaris niwa*) and White Island (*Chlorotocus*).

+ = preliminary molecular data in Van Dover et al. (2001) may indicate that the Indian Ocean (RTJ) species (*R. kairei*) is conspecific with *R. exoculata* in the Atlantic.

++ = species will need to be renamed, as another species of the genus was given this name previously; see Desbruyeres and Segonzac 1997).

* = unpublished data (J. Martin, T. Shank, M. K. Wicksten).

** = unpublished data (T. Haney, J. Martin).

Oplophoridae, Hippolytidae, Nematocarcinidae, and Pandalidae (Table 1). Only one species of endemic vent shrimp (family Alvinocarididae), *Alvinocaris lusca*, has been reported from vents in the eastern Pacific (Table 1). Three of the five vent genera are composed of species distributed in both the Atlantic and Pacific. While the range of *Rimicaris exoculata* may span two ocean basins (Atlantic and Indian; Van Dover et al. 2001; but see also Watabe & Hashimoto 2002), only shrimp species in the genus *Alvinocaris* are known to inhabit vent environments across the Pacific basin as well as in the Atlantic. Many vent sites or contiguous ridge segments host a single endemic shrimp species (e.g., *Opaepele loihi* on the Loihi Seamount and *Alvinocaris lusca* on the northern East Pacific Rise; Table 1). Prior to the discovery of the present species, only adult *Rimicaris exoculata* were known to occupy habitats on active sulfide in large numbers. An exploratory expedition (SOUEPR 1998) in November 1998 on the southern East Pacific Rise sampled biological communities on the active surface of chimneys. Chimneys were targeted primarily because the diffuse low temperature vents where shrimp are more typically found (among tube worms and mussels) on the northern EPR (and down to $\sim 17^{\circ}\text{S}$) are not present in the southern EPR.

The genus *Chorocaris* was erected by Martin and Hessler (1990) to accommodate a species of shrimp (*C. vandoverae*) collected at hydrothermal vents in the Mariana Back-Arc Basin. A previously described hydrothermal vent species, *Rimicaris chacei* Williams & Rona, 1986, from the Mid-Atlantic Ridge, was also placed in the new genus by Martin & Hessler (1990). A third species, *C. fortunata*, was described by Martin & Christiansen (1995). However, *C. fortunata* was subsequently transferred to the genus *Mirocaris* and placed in a newly erected family, the Mirocarididae, by Vereshchaka (1997). In their recent review of the genus *Mirocaris*, Komai & Segonzac (2003) recognized the validity of the genus

and confirmed that the species described as *Chorocaris fortunata* by Martin and Christiansen belonged in *Mirocaris*. However, they reduced Vereshchaka's (1997) family Mirocarididae to a synonym of the Alvinocarididae. Thus, prior to the current study there were only two known species of *Chorocaris*, one (*C. chacei*) found at sites along the Mid-Atlantic Ridge and the other (*C. vandoverae*) found at sites in the far western Pacific (Martin & Hessler 1990, Komai & Segonzac 2003).

In October of 1998, the DSV *Alvin* collected several specimens of shrimps from the Homer vent site at depths of 2573 to 2832 m along the Southern East Pacific Rise (17°S). These shrimp were living directly on the black smokers in numbers up to ~ 47 individuals per half meter square. Two of these specimens are described below as the first eastern Pacific species of *Chorocaris*. Seven additional specimens of the same species from nearby vents (all part of the Rapa Nui vent field; see Von Damm et al. 2003) are also described.

Materials and Methods

The following description is based primarily on two female specimens collected by the DSV *Alvin* on Dive 3296, 27 October 1998, from the Southern East Pacific Rise (17°S) at a depth of approximately 2596 m. These specimens were preserved in 70% ethanol and transferred from the Woods Hole Oceanographic Institution to the Natural History Museum of Los Angeles County. Additional material, consisting of 7 specimens collected on the same cruise and leg (AT-03, leg 28, 1998) but on different dives and at different sites, was discovered and examined after the initial species description was completed. These 7 additional specimens, which are not designated as paratypes, are also described and compared to the types herein. All illustrations were made using a Wild M5APO dissecting microscope. The abbreviation CL refers to carapace length (measured along



Fig. 1. *Chorocaris paulexa*, photographed on deck of *Atlantis II* shortly after collecting, included to show color pattern of a relatively fresh specimen. It is not known if this specimen was one of the two types or seven additional non-type specimens eventually transferred to the Natural History Museum of Los Angeles County. Scale bar = approximately 10.0 mm (this specimen not measured; scale bar approximated based on other measured specimens).

dorsal axis from tip of rostrum to posterior margin of carapace); TL refers to total length (rostrum to tip of telson measured along dorsal axis).

Family Alvinocarididae Christoffersen,
1986

Genus *Chorocaris* Martin and Hessler,
1990

Chorocaris paulexa, new species
Figs. 1–8

Material.—Holotype (LACM CR 1998–151.1), DSV *Alvin*, Dive 3296, 2596 m, Cruise AT-03, leg 28, 27 October 1998, Homer Vent (347°C black smoker), located at 17°37.220'S and 113°15.123'W, 2595 m, southern East Pacific Rise (17°S, 13–15.45°W), ovigerous female, CL (including rostrum) 8.5 mm, TL 27.8 mm. Paratype (LACM CR 1998-151.2), same collecting data as for holotype, female, CL 10.4 mm, TL 35.0 mm, slightly abnormal, with enlarged and distorted right antennal scale, and with inflated carapace on left side of body. Additional (non-paratype) material examined:

LACM CR 1998-152.1, 2 females, 1 ovigerous (ovigerous female CL = 10.9 mm; non-ovigerous female CL = 11.2 mm), *Alvin* Dive 3283, Southern East Pa-

cific Rise, 21–26.026°S, 114–16.626°W, 2832 m, slurp, 13 October 1998.

LACM CR 1998-153.1, 1 male (CL 8.6 mm, right side second pleopod missing), 1 female (CL = 8.6 mm, mouthparts and most legs missing), *Alvin* Dive 3292, Southern East Pacific Rise, 18–24.087°S, 113–22.657°W, 2658 m, slurp, 23 October 1998.

LACM CR 1998-154.1, 3 small specimens, 1 badly damaged with nearly all of cephalothorax missing, 1 an ovigerous female (CL = 7.3 mm), and 1 of undetermined sex (CL = 7.5 mm), *Alvin* Dive 3294, Southern East Pacific Rise, 17–25.079°S, 113–12.232°W, 2573 m, slurp, 25 October 1998.

Description.—Carapace (Figs. 1, 2, 7A).—As for the genus, with anteroventral angle slightly exceeding tip of rostrum. Rostrum broadly triangular and tapering, with distal extremity exceeding distally beyond eyes and beyond tip of suborbital spines (blunt prominences) (Fig. 2C). Dorsal half of carapace with paired slight longitudinally-oriented depressions (in holotype only); these depressions lack the minute striae seen in similar depressions in species of *Mirocaris* (see Komai and Segonzac 2003). Lateral surfaces and dorsal

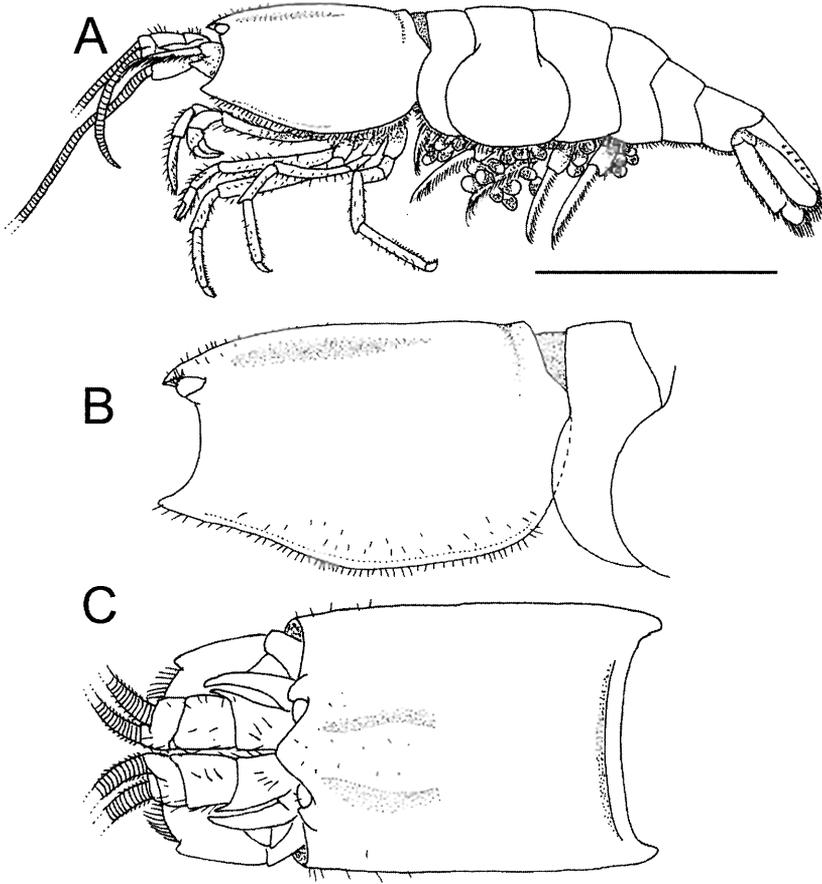


Fig. 2. *Chorocaris paulexa*, female holotype, LACM CR 1998-151.1. A, entire animal, left side. B, carapace and abdominal somite 1. C, carapace, eyes, and bases of antennules and antennae, dorsal view (flagella omitted). Scale bar = 10.0 mm for A, 5.0 mm for B and C.

anterior surface with scattered setae. Both holotype and paratype specimens rather densely covered with yellowish-brown particulate substance that fouls much of the appendages, especially where there are plumose setae.

Eyes (Fig. 2A–C).—Devoid of pigment, and with distal scattered setae.

Antennules and antennae.—Antennule (Fig. 3A–C) with 3 peduncular articles, first two approximately equal in length to each other and longer than third. Stylocerite long and acute, curving slightly inward, extending just beyond tip of lateral spine of basal segment; stylocerite bearing dorsal blunt protrusion angled slightly anteriorly, as seen in lateral view (Fig. 3B). Antennal

scale (scaphocerite) (Fig. 3D, E) broadly oval to nearly rectangular, with distal blade (lamella) extending anteriorly beyond level of anterolateral tooth; anterolateral tooth blunt, directed forward (not laterally).

Mouthparts (Fig. 3F, 4).—Mandible (Fig. 3F) with 6 sclerotized teeth on broad incisor process, with second tooth largest. Incisor process separated from unarmed and slightly upcurved molar process by wide, deep gap. Palp with two articles; setation mostly confined to distal $\frac{1}{3}$ of proximal article and dorsal border of distal article. Maxillule (first maxilla) (Fig. 4E, based on that of non-type female; holotype maxillule damaged in dissection) small in comparison to other mouthparts, with both endites strong-

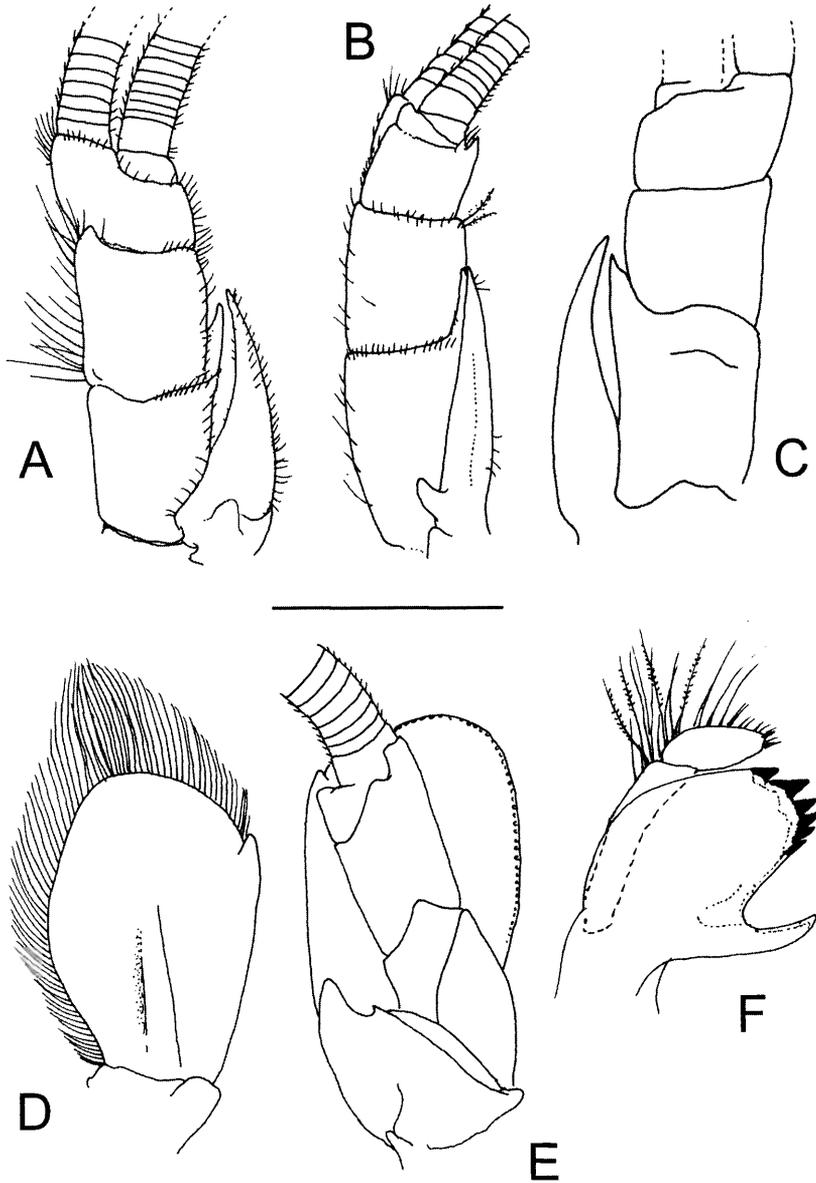


Fig. 3. *Chorocaris paulexa*, female holotype, LACM CR 1998-151.1, antennae and mandible. A, right antennular peduncle, dorsal view. B, same, lateral view (note dorsal protrusion at base of stylocerite). C, same, ventral view. D, right scaphocerite (antennal scale), dorsal view. E, antennular peduncle and scaphocerite, ventral view. F, left mandible, external (ventral) view. Scale bar = 2.0 mm for A-E; 1.0 mm for F.

ly recurved toward mouth; coxal endite distally truncated, basal endite more rounded distally and dorsally; both endites with dense rows of spines and setae; palp slightly bilobed with penultimate (proximal) lobe bearing long, thin medial process articulating with lobe, distal lobe bearing 4-5 setae.

Maxilla (second maxilla) (Fig. 4F) with broad bilobed basal endite and smaller coxal endite; both endites densely armed with short spines and setae; basal endite with dorsal tapering lash armed as illustrated; scaphognathite broad, with posterior lobe extending into and cleaning gill cham-

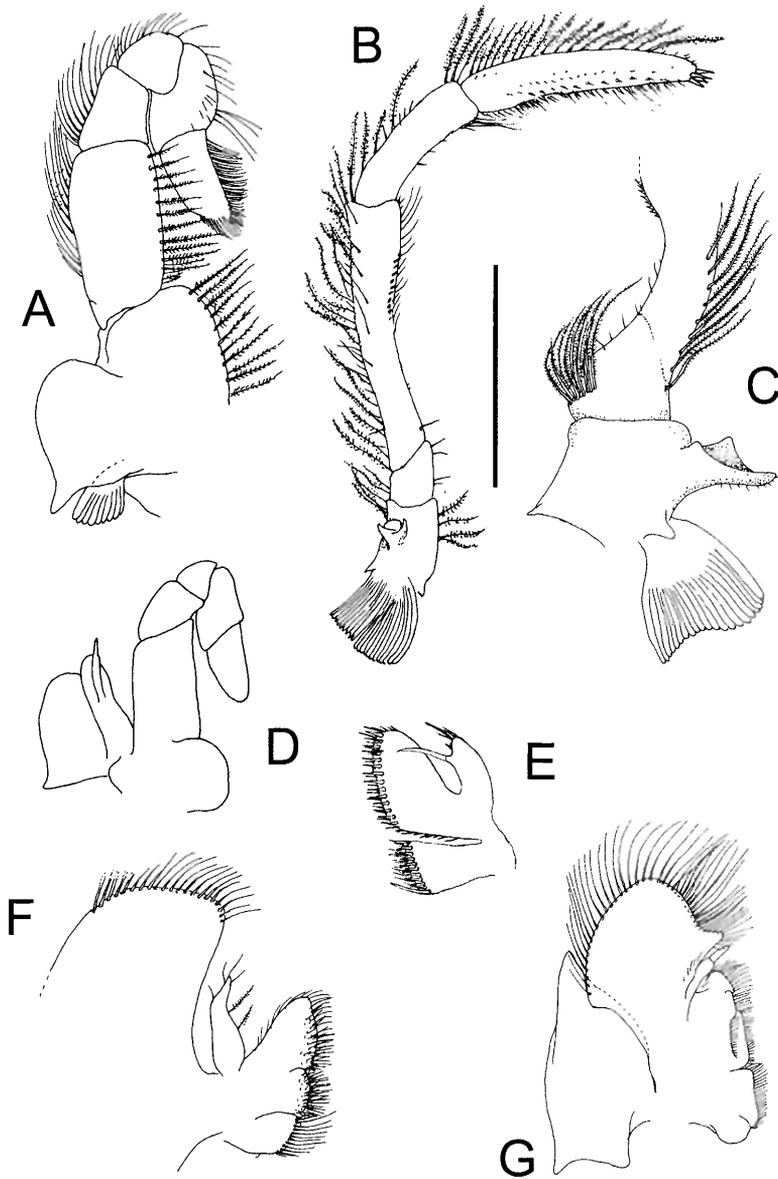


Fig. 4. *Chorocaris paulexa*, female holotype, LACM CR 1998-151.1 (A–C, F, G) and non-paratype female from Alvin dive 3283 (D, E), mouthparts. A, second maxilliped, outer view. B, third maxilliped, ventrolateral view. C, third maxilliped, coxa and proximal part of fused basi-ischial article (see text), showing close up of spatulate process extending from coxa, lateral view. D, second maxilliped of non-type female (note slight differences compared to shape of A). E, maxillule (first maxilla), outer view. F, endites of second maxilla and most of anterior lobe of scaphognathite. G, first maxilliped. Scale bar = 1.0 mm for A, C, F, G; 2.0 mm for B; other mouthparts not to scale.

ber (visible in Fig. 6). First maxilliped (Fig. 4G) with complex and heavily setose mesial endites; basal endite approximately twice size of coxal endite and composed of

what appears to be fused lobes; coxal endite with small ventral lobe; short tapering palp composed of 2 articles; exopod expanded distally and bearing dense row of plumose

setae, and with short medial rudimentary lash; epipod naked (lacking setae), tapering to acute point distolaterally and expanded and truncate proximally. Second maxilliped (Fig. 4A) with six articles; coxa broad and slightly expanded medially; epipod smaller than basis (in holotype, but not in the non-type specimen figured in 4D), rounded distally, produced into blunt point proximally; fused basi-ischium longest of articles and lined with plumose setae medially and mixed setal types distolaterally; merus short, approximately half length of basi-ischium and tapering gradually; carpus small and nearly triangular, articulating with propodus at oblique angle; propodus almost cylindrical and articulating with dactylus distally; dactylus short, basally broad, tapering distally, covered with extremely dense fields of setae on distal and distomedial surfaces. Third maxilliped (Fig. 4B, C) essentially pediform, composed of 5 articles; coxa short and with broad, distally truncate spoon-shaped lateral process (Fig. 4C); line of demarcation between the basi-ischium and ?carpus (see below) clear in ventral view only (Fig. 4B), these segments appearing fused dorsally (Fig. 4C); length of distal-most three articles (assumed here to represent the merus, carpus, and fused propodus-dactylus, though possibly representing the fused merus + carpus, propodus, and dactylus) $1 > 3 > 2$; merus (basalmost) of these articles with minute spines on distal half and with scattered plumose setae as shown; carpus (second long article) short, cylindrical; fused dactylus-propodus (terminal article) tapering distally and with dense rows of plumose setae and rows of small spines on flexor surface.

Pereopods 1 and 2 (Fig. 5 for holotype, Fig. 7 for non-type female).—First pereopod (Fig. 5A) stout, recurved, typical of genus and family (see Martin & Hessler 1990, Komai & Segonzac 2003). Dactylus thin, strongly curved, bordered by minute teeth and tipped with stout setae. Propodus curved to match dactylus, basally broad, tapering distally, with minute teeth along cut-

ting border; heel (ventro-proximal region) with 3–4 small, stout, serrate setae (arrow, Fig. 5A) that constitute part of the “carpal cleaning brush” (see Martin et al. 1998). Carpus with well developed “cleaning brush” of stout serrate setae at distal ventral border; these setae flanked by a pronounced “flange” or outgrowth of the carpus that shields them medially. Merus longer than ischium which is longer than basis. All articles with setae as illustrated. First pereopod of non-type specimens more robust (see below under variation). Second pereopod (Fig. 5B) with fingers of chela just crossing at tips and with both fingers bearing minute teeth along cutting borders. Dactylus slightly more than half length of propodus. Carpus shorter than merus and approximately equal in length to ischium. All articles fairly heavily setose as illustrated.

Pereopods 3–5 (Figs. 5D–F, 6).—Similar to one another. No epipods or setobranch setae present. Dactylus (Fig. 5D) very short, strongly recurved, and bearing cluster of sclerotized spines on flexor surface; spines not arranged in obvious rows. Propodus bearing minute movable spines along flexor surface, most noticeable along distal half. Carpus with distodorsal border strongly produced and slightly overhanging proximal $\frac{1}{7}$ to $\frac{1}{8}$ of propodus. Merus longer than propodus which is longer than carpus. Branchial formula (Fig. 6) consisting of arthrobranchs and pleurobranchs on pereopods 1 through 4; pereopod 5 with pleurobranch only; maxilliped 3 with arthrobranch only.

Pleopods (Fig. 8B).—Exopod and endopod similar in shape, with exopod slightly longer than endopod. Protopod with strong, sharp carina along its posterior surface and extending along its length. Endopod bearing small, simple appendix interna (Fig. 8C) lacking cincinnuli.

Abdomen (Fig. 2A).—Typical for genus, unremarkable.

Telson and uropods (Fig. 8A, D).—Telson with roughly parallel borders diverging slightly anteriorly and with 5 to 8 pairs of

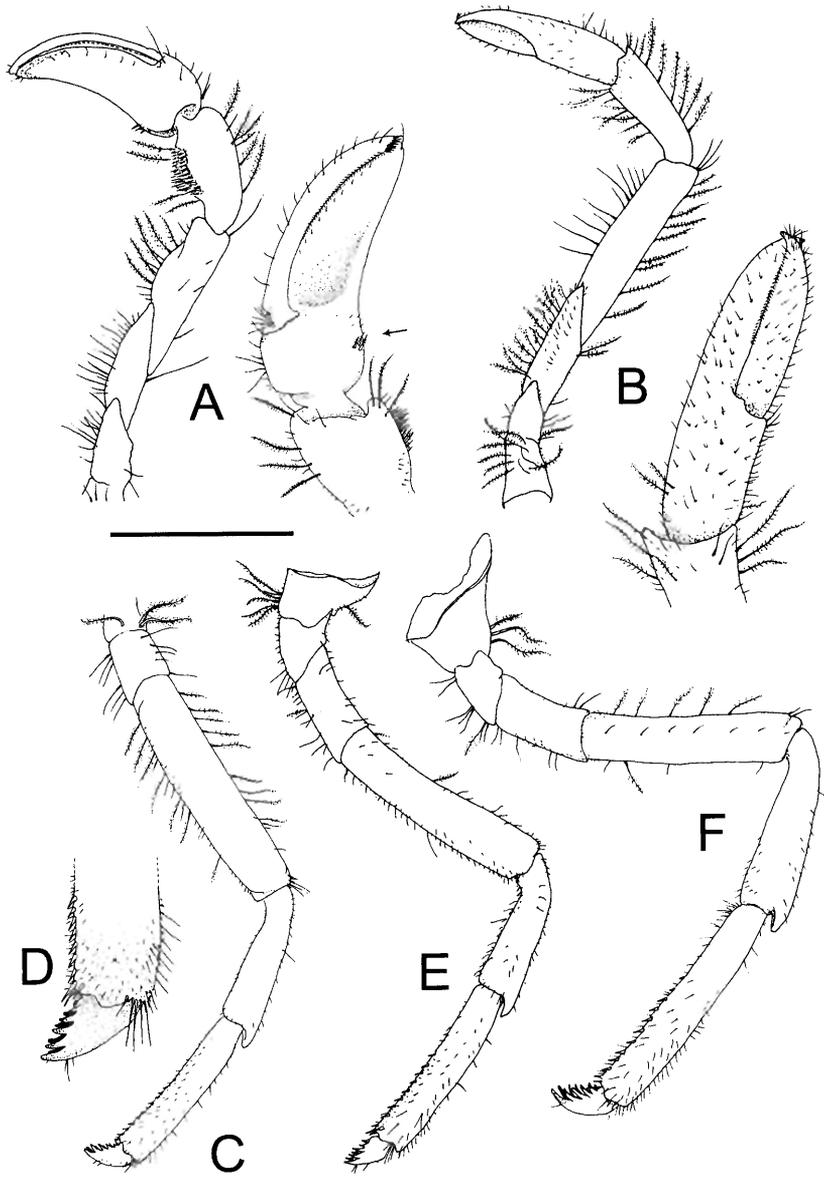


Fig. 5. *Chorocaris paulexa*, female holotype, LACM CR 1998-151.1, pereopods. A, first pereopod (cheliped), lateral view, entire appendage (on left) and higher magnification of chela and carpus in mesial view (on right). B, second pereopod, mesial view of entire appendage (on left) and higher magnification of chela and part of carpus in lateral view (on right). C, third pereopod, lateral view. D, higher magnification of dactylus and distal region of propodus of third pereopod. E and F, fourth and fifth pereopods, respectively. Scale bar = 2.0 mm for A, B, C-F; 1.0 mm for D and for enlargements (chela) of A and B.

short, stout, movable spine-like setae in addition to pair of movable spine-like setae at each posterodistal corner (holotype and paratype both with uneven number as illustrated; holotype with 6 + 2 spines on one

side but 8 + 2 spines on other; paratype with 6 + 2 and 5 + 2 spines). Posterior margin of telson broadly rounded, terminating in row of stout plumose setae between the pair of "corner" spines described

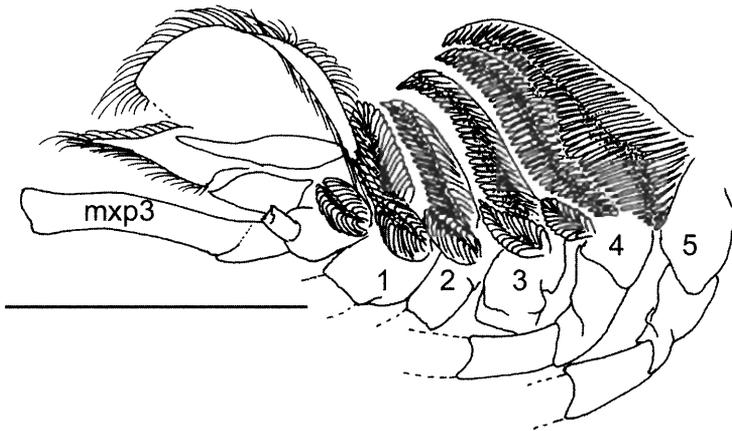


Fig. 6. *Chorocaris paulexa*, branchial formula and location, Lateral view of non-paratype female from *Alvin* dive 3283 with portion of left side carapace removed, showing large pleurobranch gills (on pereopods 1–5) and smaller, more oval, and more basally located arthrobranch gills (on third maxilliped and pereopods 1–4). Arabic numerals refer to pereopods 1–5; mxp3 = third maxilliped. Note absence of epipods on coxa of all pereopods. Scale bar = 5.0 mm.

above. Uropods both gently rounded distally; exopod slightly longer than endopod and bearing two movable spines at outer border of diaresis (arrow, Fig. 8D); diaresis interrupted at approximate midline of uropod (Fig. 8A).

Eggs.—The holotype is carrying a large number of eggs (Fig. 2A); at least 40 of these are visible but the exact number cannot be determined without dissection and damage to the specimen. Each egg measures approximately 0.74 mm long and 0.50 mm wide and is polarized, with $\frac{1}{3}$ to $\frac{1}{2}$ of the egg lighter colored than the rest of the egg and separated by a fairly clear demarcation line.

Color (Fig. 1).—Live shrimp mostly pale translucent white to slightly pink on posterior and dorsal surfaces of carapace and abdomen. Anteroventral region of carapace, especially area overlying gills, dark red to nearly black; some dark pigmentation on bases of pereopods and along ventral abdominal border. Dorsal region of carapace behind eyes (region corresponding to hepatopancreas) light yellow-orange. In alcohol, nearly uniformly beige but with yellowish- to orange-brown particulate substance on appendages giving overall yellow

to ochre appearance to types; other specimens differing in presence of type of attached particulate matter (see below). Sclerotized spines of dactyls appearing dark, almost black. Some non-type material appearing more gray-white than the two type specimens (see below).

Etymology.—The name *paulexa*, used as a noun in apposition, is an amalgamation of the first names of Paul Martin and Alexandra (Alex) Martin, children of the first author. Like each child, the new species is fragile, rare, and beautiful, and fills us with a sense of awe and wonder.

Variation.—The two specimens that constitute the type series differ from some of the 7 non-type specimens, all of which were collected from the southern East Pacific Rise on the same leg and cruise (28, AT-03) as the types and came to our attention after the types had been described and illustrated. Size of the non-types ranges from 7.3 mm CL (an ovigerous female) to 11.4 mm CL (a non-ovigerous female), thus encompassing the size range of the holotype and paratype (8.5 mm and 10.4 mm CL, respectively). The largest known specimen, illustrated in Figures 6, 7A–E, and 8D, is a non-ovigerous female. Morphological vari-

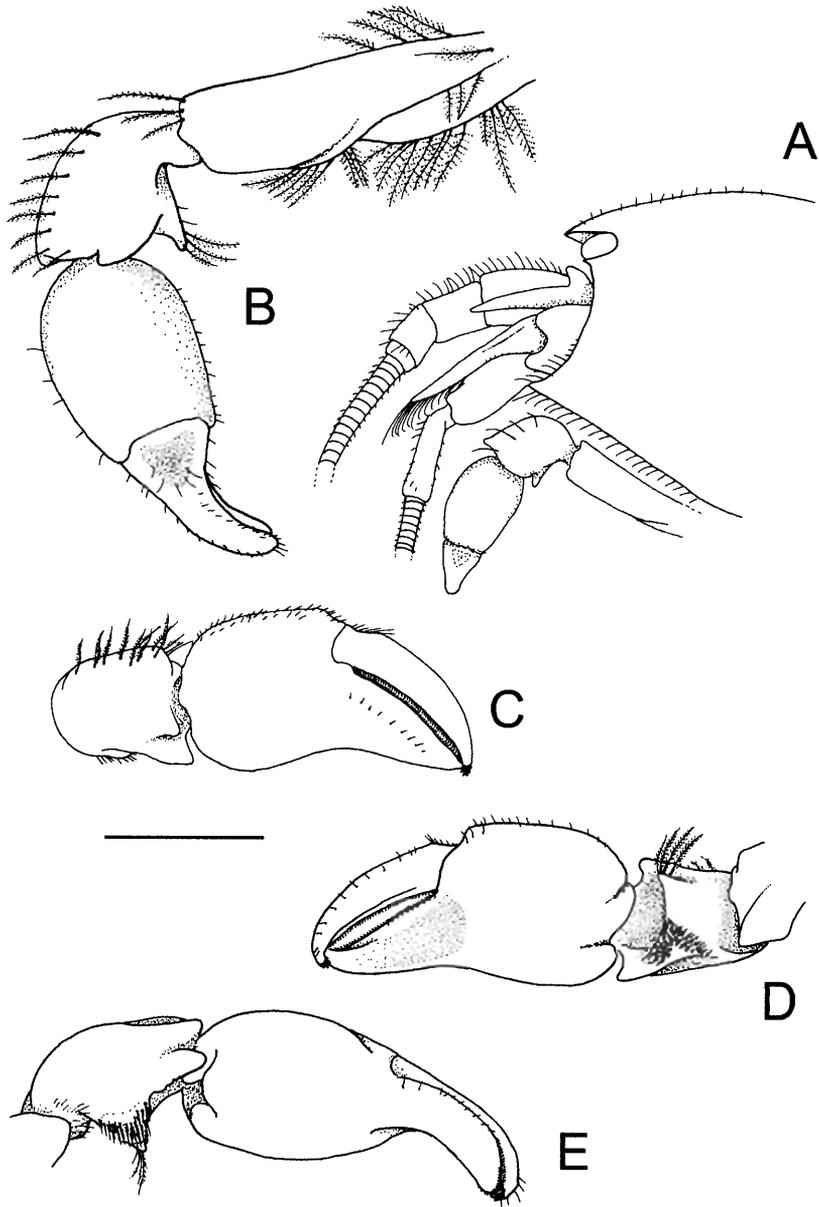


Fig. 7. *Chorocaris paulexa*, non-paratype female from *Alvin* dive 3283. A, anterior region of carapace with pereopod 1 (cheliped) shown in situ. B, entire cheliped, dorsal view. C, chela in outer view. D, chela in inner view. E, chela, ventral view. Scale bar = 4.0 mm for A, 2.0 mm for B–E.

ation was greatest in the overall form of the first pereopod (cheliped). In the two type specimens, the chela is slightly recurved, as is the case with all alvinocaridids, but the cheliped overall is slender and somewhat delicate (Fig. 5A). The stout serrate setae of the cleaning brush on the carpus are mir-

rrored by three small similar cleaning setae on the ventral margin of the palm (these setae are known to change with ontogeny in some species; see Martin et al. 1998). In contrast, the two females from *Alvin* Dive 3283 have a far more robust and inflated chela, and the overall appearance of the

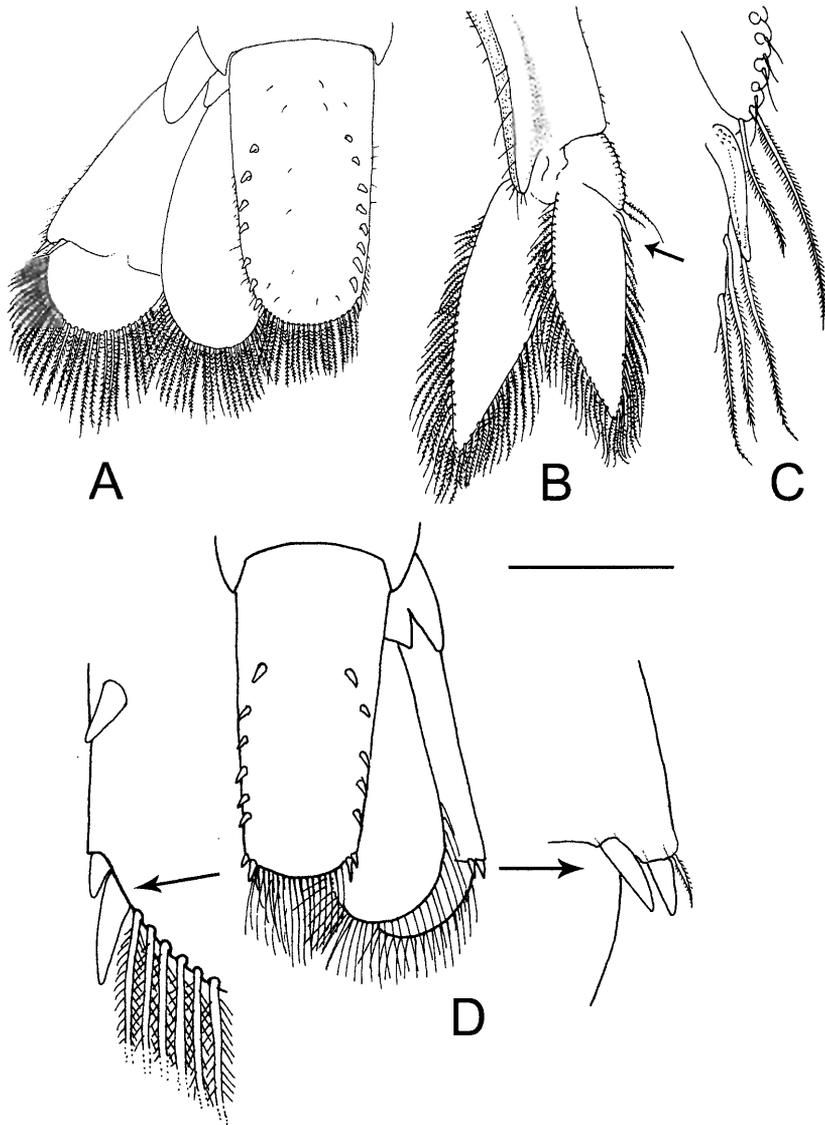


Fig. 8. *Chorocaris paulexa*, telson and pleopods. A, telson of female holotype, LACM CR 1998-151.1, dorsal view. B, pleopod of paratype, LACM, posterior view. C, higher magnification of appendix interna of pleopod 2 denoted by arrow in B. D, telson and right uropods of non-paratype female from *Alvin* dive 3283 and enlargements of spines of the telson (to the left) and outer uropod (arrow to right). Scale bar = 2.0 mm for A, B; 0.75 mm for C; 4.0 mm for D; enlargements of D not to scale.

cheliped is more stout (Fig. 7). Additionally, there are no serrate setae on the palm of the cheliped opposite the stout setae of the carpal cleaning brush. It is possible that the species exhibits polymorphism in the first pereopod, as has also been reported for another alvinocaridid, *Alvinocaris longirostris*, by Kikuchi & Ohta (1995). The form

of the telson is also slightly different in the non-types, which have a somewhat more truncate posterior telson border (Fig. 8D). The number of paired spines on the telson varies both between and within specimens (as noted above and shown in Figs. 8A, D). This overall more robust form is exhibited by both specimens from *Alvin* Dive 3283

and both specimens from *Alvin* Dive 3292. The three specimens from *Alvin* Dive 3294 all are much smaller than the remaining specimens, with the largest having a CL of only 7.5 mm. These three small shrimp are more slender than the above specimens and therefore are more similar to the two type specimens. Despite the fact that the holotype female is ovigerous (and in fact the smallest specimen from Dive 3294 (at 7.3 mm CL) is also ovigerous), it is possible that these specimens (the types plus the three specimens from Dive 3294) are nevertheless not "mature" in the sense of the robust form that the larger specimens seem to attain.

In addition to the morphological variation noted above, the three small specimens from *Alvin* Dive 3294 are all quite clean, completely lacking the rust-colored fouling material associated with the types, and were a very pale grayish color as opposed to the darker beige or tan of the other specimens. The larger specimens from dives 3283 and 3292 also lacked the orange-brown flocculent debris described for the two type specimens, and instead carried black or dark gray debris on the setae and appendages (especially the two specimens from dive 3283). We attribute this difference to minor differences in microhabitat. All of the ovigerous females exhibited the slight longitudinal indentations on either side of the carapace midline as depicted in Fig. 2A.

Because only nine specimens are available for examination, and because morphological variation is now known to be common in alvinocaridid shrimps (e.g., Kkuchi & Ohta 1995), it is premature to speculate as to whether these slight differences are sufficient to question the species assignment of the seven non-type specimens. We have chosen the conservative approach of assigning type status to only the two above-mentioned females, assuming at this time that the additional seven specimens are members of the same species but not designating them as paratypes.

Remarks.—Morphologically, *Chorocaris*

paulexa is strikingly similar to the other two species of *Chorocaris*. This morphological similarity within the genus is remarkable considering the great distance separating the known species. *Chorocaris paulexa* differs from both *C. vandoverae* and *C. chacei* in having a more acute branchiostegal angle (projection) of the carapace. The new species differs from *C. vandoverae* in having a slightly more acute rostrum in dorsal view, a longer merus of the second pereopod (relative to the ischium), and a more acute (though still quite blunt) anterolateral tooth on the antennal scale. *Chorocaris paulexa* differs from *C. chacei* in having a rostrum that clearly exceeds the anteriormost projection of the postorbital prominences (in *C. chacei* the rostrum barely reaches or falls short of these prominences). *Chorocaris paulexa* also differs from both *C. vandoverae* and *C. chacei* in having slightly indented regions on either side of the midline of the carapace, similar to what has been described as a defining character of the genus *Mirocaris* by Komai & Segonzac (2003) but lacking the striations in these regions seen in *Mirocaris* (see Komai & Segonzac 2003). These depressed regions apparently occur only in ovigerous females, as is also the case with *Mirocaris* according to Komai & Segonzac (2003). Other apparent differences between *C. paulexa* and either *C. chacei*, or *C. vandoverae* are so slight as to be possibly ascribed to intraspecific variation. Indeed, T. Komai, after having examined numerous samples of *C. vandoverae* and *C. chacei* as well as the holotype and paratype of *C. paulexa*, feels that the only consistent character separating the three species is the shape of the pterygostomial angle (T. Komai, pers. com.). With only nine specimens of the new species available for examination, the amount of morphological variation is difficult to assess (see earlier comments on variation); slight differences may even be caused by differences in interpretation or illustration. Therefore, we are currently investigating the systematic and evolutionary relation-

ship of *C. paulexa* with other alvinocaridid shrimp using molecular genetic techniques on frozen specimens to examine evolutionary hypotheses. Based entirely on morphology, we hypothesize that *C. paulexa* is more closely related to *C. vandoverae* than it is to *C. chacei* in the Atlantic.

The only other vent-endemic shrimp on the SEPR is *Alvinocaris lusca*, but that species occurs only among the low-temperature diffuse flow communities (*Riftia* assemblages and mussel beds) and not on the sides of high temperature vents. *Chorocaris paulexa* did not exhibit the "clustering" or "swarming" behavior or abundance of *Rimicaris exoculata* on the MAR. The northern limit of *C. paulexa* is 17.5°S, and the southern limit is 22.5°S (although apparently it is documented in archived video from 32°S), increasing in abundance with distance to the south (from a few individuals to up to ~47 individuals/0.5 m²). Thus, *C. paulexa* on the SEPR occupies a similar physical niche to that of *R. exoculata* in the Mid-Atlantic. Perhaps it also occupies a similar ecological niche, consuming bacteria off the sides of active smokers, although there are no obvious morphological adaptations (such as the inflated carapace of *Rimicaris*) that might suggest this. *Rimicaris exoculata* is known to "farm" a relative monoculture of bacteria in its gill chambers and appendages (Gebruk et al. 1997, Polz et al. 1998). The observed yellowish-brown particulate substance that fouls much of the appendages may be indicative of a similar feeding pattern in *C. paulexa*, though this was not seen on all specimens. It should be noted that the typical abundance of diffuse flow habitats (non-chimney) significantly decreases from 18° to 22.5°S. Indeed, there are no non-chimney-related diffuse flow habitats at 22.5°S, where the greatest abundance of *C. paulexa* was documented (Brandon vent area, Von Damm et al. 2003). The geographic separation of *Chorocaris* species is also noteworthy, with the closest (to *C. paulexa*) species of the genus being *C. vandoverae* in the western Pacific.

Thus, our report extends the known range of the genus *Chorocaris* approximately 11,000 km eastward (from the Mariana Back-Arc Basin), virtually across the entire Pacific Ocean.

The biological characterization of the Rapa Nui field (22.5°S) in October 1998 was largely limited to the area (<20 m) associated with the high temperature vents due to the absence of diffuse venting and the unusual chemistry of the high temperature fluids (Von Damm et al. 2003). Clusters of *Chorocaris paulexa* roaming on the side and top of the Rapa Nui smokers, as well as chirotidid holothurians, eosiphoid gastropods, and large grievellid copepods at the base of the smokers, were observed and sampled. Unlike communities between 7°–18°S and at 32°S, no riftiid tubeworms, bathymodiolid mussels, or vesicomid clams were observed in the Rapa Nui field. Subsequently, each of the Rapa Nui species above has shown affinities for close morphological relationships to northwestern or southeastern Pacific vent faunas and are now hypothesized to have their closest relatives in these regions (Smirnov et al. 2000, Waren & Bouchet 2001, Ferrari et al. 2000, Shank, unpublished data). Such evolutionary patterns would be consistent and parallel with what has been documented in non-vent deep-sea fauna (Vinogradov 1997) and hypothesized for deep-sea hydrothermal vent fauna (Mironov et al. 1998, Smirnov et al. 2000). Based on these patterns we hypothesize that 1) *Chorocaris paulexa* is a distinct species from *C. vandoverae* and *C. chacei*, 2) *C. paulexa* is more closely related to *C. vandoverae* than to *C. chacei*, and 3) *C. paulexa* has evolved to black smoker habitats. We are currently testing these hypotheses using molecular phylogenetic analysis.

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Literature Cited

- Christoffersen, M. L. 1986. Phylogenetic relationships between Oplophoridae, Atyidae, Pasiphaeidae, Alvinocarididae fam. n., Bresiliidae, Psalidopodidae and Disciadiidae (Crustacea Caridea Atyoidea).—*Bolletim de Zoologia* 10:273–281.
- Desbruyères, D., & M. Segonzac (eds). 1997. Handbook of deep-sea hydrothermal vent fauna. Editions IFREMER, Brest, 279 p.
- Ferrari, F. D., & E. L. Markhaseva. 2001. *Grievella shanki*, a new genus and species of scolecitrichid calanoid copepod (Crustacea) from a hydrothermal vent along the southern East Pacific Rise.—*Proceedings of the Biological Society of Washington* 114:348–348.
- Fowler, C. M. R., & V. Tunnicliffe. 1997. Hydrothermal vent communities and plate tectonics.—*Endeavour* 21:164–168.
- Gebruk, A. V., S. V. Galkin, A. L. Vereshchaka, L. I. Moskalev, & A. J. Southward. 1997. Ecology and biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge.—*Advances in Marine Biology* 32:93–144.
- Hayashi, K., & S. Ohtomi. 2001. A new species of the genus *Periclimenes* (Decapoda: Caridea: Palaeomonidae) collected from hydrothermal vent fields in Kagoshima Bay, Japan.—*Crustacean Research* 30:160–171.
- Kikuchi T., & S. Ohta. 1995. Two caridean shrimps of the families Bresiliidae and Hippolytidae from a hydrothermal field on the Iheya Ridge, off the Ryukyu Islands, Japan.—*Journal of Crustacean Biology* 15:771–785.
- Komai, T., & M. Segonzac. 2003. Review of the hydrothermal vent shrimp *Mirocaris*, redescription of *M. fortunata* and reassessment of the taxonomic status of the family Alvinocarididae (Crustacea: Decapoda: Caridea).—*Cahiers de Biologie Marine* 44:199–215.
- , & ———. 2004. A new genus and species of alvinocarid shrimp (Crustacea: Decapoda: Caridea) from hydrothermal vents on the North Fiji and Lau Basins, south-western Pacific.—*Journal of the Marine Biological Association of the United Kingdom* 84:1179–1188.
- Martin, J. W. 2003. Oplophorid shrimp (Decapoda, Caridea) from an Arctic hydrothermal vent.—*Crustaceana* 76:871–878.
- , & J. C. Christiansen. 1995. A new species of the shrimp genus *Chorocaris* Martin and Hessler, 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents along the Mid-Atlantic Ridge.—*Proceedings of the Biological Society of Washington* 108:220–227.
- , & G. E. Davis. 2001. *An Updated Classification of the Recent Crustacea*. Natural History Museum of Los Angeles County, Science Series 39:1–124.
- , & T. A. Haney. In press. Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2004.—*Zoological Journal of the Linnean Society*.
- , & R. R. Hessler. 1990. *Chorocaris vandoverae*, a new genus and species of hydrothermal vent shrimp from the Western Pacific.—*Contributions in Science, Natural History Museum of Los Angeles County* 417:1–11.
- , J. Signorovitch, & H. Patel. 1998. Comparison of the carpal cleaning brush in two genera of hydrothermal vent shrimp (Crustacea, Decapoda, Bresiliidae).—*Journal of Morphology* 235:31–39.
- Mironov, A. N., A. V. Gebruk, and L. I. Moskalev. 1998. Biogeographical patterns of the hydrothermal vent fauna: a comparison with 'non-vent biogeography'.—*Cahiers de Biologie Marine* 39:367–368.
- Polz, M. F., J. J. Robinson, C. M. Cavanaugh, & C. L. Van Dover. 1998. Trophic ecology of massive shrimp aggregations at a Mid-Atlantic Ridge hydrothermal vent site.—*Limnology and Oceanography* 43(7):1631–1638.
- Shank, T. M., M. B. Black, K. M. Halanych, R. A. Lutz, & R. C. Vrijenhoek. 1999. Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochon-

- drial cytochrome oxidase subunit I.—Molecular Phylogenetics and Evolution 13:244–254.
- , R. A. Lutz, & R. C. Vrijenhoek. 1998. Molecular systematics of shrimp (Decapoda: Bresiliidae) from deep-sea hydrothermal vents, I: enigmatic “small orange” shrimp from the Mid-Atlantic Ridge are juvenile *Rimicaris exoculata*.—Molecular Marine Biology and Biotechnology 7:88–96.
- , & J. W. Martin. 2003. A new caridean shrimp of the family Alvinocarididae from thermal vents at Menez Gwen on the Mid-Atlantic Ridge.—Proceedings of the Biological Society of Washington 116:158–167.
- Smirnov, A. V., A. V. Gebruk, S. V. Galkin, & T. Shank. 2000. New species of holothurian (Echinodermata: Holothuroidea) from hydrothermal vent habitats.—Journal of the Marine Biological Association of the United Kingdom 80:321–328.
- Van Dover, C. L. 1995. Ecology of Mid-Atlantic Ridge hydrothermal vents. Pp. 257–294 in L. M. Parson, C. L. Walker, & D. R. Dixon, eds., Hydrothermal vents and processes, Geological Society of America Special Publication 87.
- , S. E. Humphris, D. Fornari, C. M. Cavanaugh, R. Collier, S. K. Goffredi, J. Hashimoto, M. D. Lilley, A. L. Reysenbach, T. M. Shank, K. L. Von Damm, A. Banta, R. M. Gallant, D. Gotz, D. Green, J. Hall, T. L. Harmer, L. A. Hurtado, P. Johnson, Z. P. McKiness, C. Meredith, E. Olson, I. L. Pan, M. Turnipseed, Y. Won, et al. 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents.—Science 294(5543):818–823.
- Vereshchaka, A. L. 1996a. Comparative analysis of taxonomic composition of shrimps as edificators of hydrothermal communities in the Mid-Atlantic Ridge.—Doklady Biological Sciences 351:576–578.
- . 1996b. A new genus and species of caridean shrimp (Crustacea: Decapoda: Alvinocarididae) from North Atlantic hydrothermal vents.—Journal of the Marine Biological Association of the United Kingdom 76:951–961.
- . 1997. A new family for a deep-sea caridean shrimp from North Atlantic hydrothermal vents.—Journal of the Marine Biological Association of the United Kingdom 77:425–438.
- Vinogradova, N. G. 1997. Zoogeography of the abyssal and hadal zones.—Advances in Marine Biology 32:325–388.
- Von Damm, K. L., M. D. Lilley, W. C. Shanks III, M. Brockington, A. M. Bray, K. M. O’Grady, E. Olson, A. Graham, G. Proskurowski, T. M. Shank, R. Collier, J. Cowen, R. Haymon, M. K. Tivey, D. Fornari, K. Nakamura, E. McLaughlin-West, J. Kaye, J. Sarrazin, & B. Cushman. 2003. Extraordinary phase separation and segregation in vent fluids from the southern East Pacific Rise.—Earth and Planetary Science Letters 206:365–378.
- Waren, A., & P. Bouchet. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records.—Veliger 44:116–23.
- Watabe H., & J. Hashimoto. 2002. A new species of the genus *Rimicaris* (Alvinocarididae: Caridea: Decapoda) from the active hydrothermal vent field, “Kairei field,” on the Central Indian Ridge, the Indian Ocean.—Zoological Science 19:1167–1174.
- Webber, R. 2004. A new species of *Alvinocaris* (Crustacea: Decapoda: Alvinocarididae) and new records of alvinocaridids from hydrothermal vents north of New Zealand.—Zootaxa 444:1–26.
- Williams, A. B. 1988. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage.—Fishery Bulletin 86:263–287.
- , & F. A. Chace, Jr. 1982. A new caridean shrimp of the family Bresiliidae from thermal vents of the Galapagos Rift.—Journal of Crustacean Biology 2:136–147.
- , & F. C. Dobbs. 1995. A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii.—Proceedings of the Biological Society of Washington 108:228–237.
- , & P. A. Rona. 1986. Two new caridean shrimps (Bresiliidae) from a hydrothermal field on the Mid-Atlantic Ridge.—Journal of Crustacean Biology: 446–462.

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