

## TAXONOMIC REVIEW OF THE HYDROTHERMAL VENT SHRIMP GENERA *RIMICARIS* WILLIAMS & RONA AND *CHOROCARIS* MARTIN & HESSLER (CRUSTACEA: DECAPODA: CARIDEA: ALVINOCARIDIDAE)

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**ABSTRACT** A taxonomic review of the two genera of the family Alvinocarididae (Decapoda: Caridea), *Rimicaris* Williams and Rona, 1986 and *Chorocaris* Martin and Hessler 1990, is presented based on study of type materials and/or supplemental material from recent collections. Two species of *Rimicaris*, *R. exoculata* Williams and Rona 1986 and *R. kairei* Watabe and Hashimoto 2002, and three species of *Chorocaris*, *C. chacei* Williams and Rona 1986, *C. vandoverae* Martin and Hessler 1990, and *C. paulexa* Martin and Shank 2005, are recognized. All species are exclusively associated with deep-water hydrothermal community. Close relationship between the two genera is confirmed by morphological characters, but the monophyly of *Chorocaris* is not corroborated. An examination of a good series of material from the Mid-Atlantic Ridge shows that juveniles of *Rimicaris exoculata* can be arranged in four sequential ontogenetic stages based on morphology. A dramatic change occurs at the size of 7.0 to 9.0 mm in the carapace length. The synonymies of *Iorania concordia* Vereshchaka 1996 and *Rimicaris aurantiaca* Martin, Signorovitch & Patel 1997 with *Rimicaris exoculata*, indicated from molecular evidence by Shank et al. (1998), are confirmed. Morphological differences between *R. exoculata* and *R. kairei* and those among *C. chacei*, *C. vandoverae*, and *C. paulexa*, are reassessed.

**KEY WORDS:** Crustacea, Decapoda, Caridea, Alvinocarididae, *Rimicaris*, *Chorocaris*, taxonomy, hydrothermal vents

### INTRODUCTION

Species of the caridean shrimp family Alvinocarididae exclusively occur in reducing habitats in deepwater, (i.e., hydrothermal vents or cold water sulfide/hydrocarbonseeps. At present, they are classified into 7 genera, including *Alvinocaris* Williams and Chace 1982, *Chorocaris* Martin and Hessler 1990, *Mirocaris* Vereshchaka 1997, *Nautilocaris* Komai and Segonzac 2004, *Opaepele* Williams and Dobbs 1995, *Rimicaris* Williams and Rona 1986, and *Shinkaicaris* Komai and Segonzac 2005 (Komai & Segonzac 2003, Komai & Segonzac 2004, Komai & Segonzac 2005, Martin & Haney 2005). Komai and Segonzac (2003) did not recognize Mirocarididae, originally proposed by Vereshchaka (1997a) to accommodate the genus *Mirocaris*, because the presence of possible synapomorphies strongly suggests that *Mirocaris* is subordinated in Alvinocarididae.

*Rimicaris* was originally established for two species discovered from hydrothermally influenced vent field, TAG (Tans-Atlantic Geotraverse) on the MAR (Mid-Atlantic Ridge), *Rimicaris exoculata* Williams and Rona 1985 and *R. chacei* Williams and Rona 1986 (Williams & Rona 1986). The former was designated as the type species of the genus. Later, Martin and Hessler (1990) described a new genus, *Chorocaris*, for a new species *C. vandoverae* (the type species of the genus) from hydrothermal vents along the Back-Arc Spreading Center in the western Pacific, and transferred *Rimicaris chacei* to *Chorocaris*. Martin and Christiansen (1995) described a new species, *Chorocaris fortunata*, from Lucky Strike on the MAR, but this species was later transferred to *Mirocaris* by Vereshchaka (1997a). Martin et al. (1997) described a new taxon, *Rimicaris aurantiaca* Martin, Signorovich and Patel 1997, as the second representative of *Rimicaris* based on material from Snake Pit vent field on the MAR, but the subsequent genetic studies

suggested that the taxon was founded from juvenile of *R. exoculata* (Shank et al. 1998, Shank et al. 1999). Similarly, it was indicated that the genus *Iorania* Vereshchaka 1996, and the type species *I. concordia* Vereshchaka 1996, described from the TAG, were founded on juveniles of *R. exoculata*. Hashimoto et al. (2001) first mentioned the presence of species of *Rimicaris* at hydrothermal vent field on the Rodriguez Triple Junction on the Central Indian Ridge, Indian Ocean, and almost at the same time Van Dover et al. (2001) reported *R. aff. exoculata* and *Chorocaris* sp. from the same area. Watabe and Hashimoto (2002) formally described the *Rimicaris* species as new, *R. kairei*. The existence of a species of *Chorocaris* in the Indian Ocean has not been confirmed until now. Martin and Shank (2005) described a new species, *Chorocaris paulexa* Martin and Shank 2005, from Rapa Nui Homer Vent Site on the southern East Pacific Rise (EPR). At present, *Rimicaris* and *Chorocaris* are represented by two (*R. exoculata* and *R. kairei*) and three species (*C. vandoverae*, *C. chacei*, and *C. paulexa*), respectively. *Rimicaris exoculata* and *Chorocaris chacei* are widespread along the MAR in the northern hemisphere, whereas the other three species seem to be restricted to the type and/or nearby localities, although the density of population is sometimes very high (Martin & Haney 2005). *Rimicaris exoculata* is one of the most extensively studied vent crustaceans to date. A large number of articles, dealing with various aspects of biology, including morphology, ecology, behavior, and physiology has been published (see review by Martin & Haney 2005).

This study was initiated to identify material from various vent sites on the MAR. Two species, *Rimicaris exoculata* and *Chorocaris chacei*, were identified, but a wide range of morphological variation observed led us to question reliability of morphological characters used by previous authors for species discrimination. Furthermore, a good series of material covering various postlarval stages enabled us to investigate ontogenetic changes of *R. exoculata* and *C. chacei*. Consequently,

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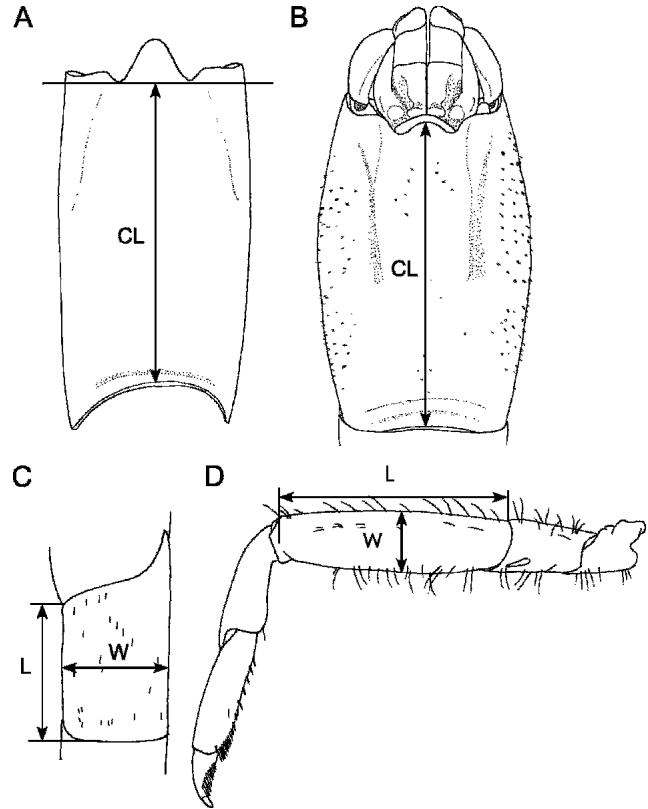
we decided to review all described species of *Rimicaris* and *Chorocaris*. As a result, two species of *Rimicaris* (*R. exoculata* and *R. kairei*) and three species *Chorocaris* (*C. chacei*, *C. vandoverae*, and *C. paulexa*) are confirmed to be valid. It has been also confirmed that *R. exoculata*, and probably *R. kairei*, undergo dramatic ontogenetic changes at early postlarval stages. Based on examination of morphology, four sequential stages are categorized for juveniles of *R. exoculata*. *Rimicaris aurantiaca* and *Iorania concordia* both correspond to one of these stages, and therefore the synonymy of these two taxa with *R. exoculata* is fully verified. Reexamination of type material has disclosed that juveniles of *Rimicaris exoculata* were mixed in the juvenile paratypes of *Chorocaris chacei*, and the error is corrected here. Most diagnostic characters for species discrimination, used by previous authors, are found to be more or less subject to intraspecific or ontogenetic variation. We have attempted to find new characters useful for species discrimination.

#### MATERIAL AND METHODS

The type material was obtained on loan (see acknowledgments). Newly obtained collections studied here came from several diving cruises organized by French, Japanese, American, and German teams: HYDROSLAKE, DS *Nautilé*/RV *L'Atalante*, June 1988 (chief scientist C. Mével), Mid-Atlantic Ridge (MAR), Snake Pit (3,500 m); DIVA 2, DS *Nautilé*/RV *L'Atalante*, June 1994 (chief scientist D. Desbruyères), MAR, Menez Gwen; MICROSMOKE, DSV *Nautilé*/RV *L'Atalante*, November 1995 (chief scientist D. Prieur), Snake Pit; ATOS, ROV *Victor*/RV *L'Atalante*, July 2001 (chief scientist P.-M. Sarradin), MAR, Lucky Strike (1,700 m) and Rainbow (2,300 m); PICO, DS *Nautilé*/RV *Nadir*, July 1998 (chief scientist D. Desbruyères), MAR Rainbow (2,300 m) and Lucky Strike (1,650 m); ATOS, ROV *Victor 6000*/RV *L'Atalante*, July 2001 (chief scientist P.-M. Sarradin), MAR, Lucky Strike (1,700 m); DiversExpedition, DS *Alvin*/RV *Atlantis*, July 2001 (chief scientist C.L. Van Dover), MAR, Logatchev (3,010 m); ROV *Kaiko*/RV *Kairei*, February 2002 (chief scientist J. Hashimoto), and YK01-15, DS *Shinkai 6500*/RV *Yokosuka*, 2002 (chief scientist J. Hashimoto), Kairei Field, Central Indian Ridge; EXOMAR, ROV *Victor 6000*/RV *L'Atalante*, August 2005 (chief scientist A. Godfroy), MAR, TAG (3,650 m), Rainbow (2,300 m) and Lucky Strike (1,700 m); MOMARETO, ROV *Victor 6000*/RV *Pourquoi Pas?*, September 2006 (chief scientists J. Sarrazin & P.-M. Sarradin), MAR, Rainbow (2,300 m) and Lucky Strike (1,700 m); M68/1, ROV *Quest 4000*/RV *Meteor*, May 2006 (chief scientist A. Koschinsky); SERPENTINE, ROV *Victor 6000*/RV *Pourquoi Pas?*, March 2007 (chief scientist Y. Fouquet).

The material examined is deposited in the collections in the following institutions: Japan Marine Science and Technology Center, Yokosuka (JAMSTEC); Muséum national d'Histoire naturelle, Paris (MNHN); Natural History Museum and Institute, Chiba (CBM); Natural History Museum of Los Angeles County (LACM); National Museum of Natural History, Smithsonian Institution (USNM); Zoologisches Institut und Zoologisches Museum, Hamburg, Germany (ZMH).

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 primarily provided by the post-orbital carapace length (PCL), measured from the level of the



**Figure 1.** Diagrammatic *Rimicaris*, showing measurements used in text. (A) Carapace in dorsal view, postorbital carapace length used for *Chorocaris* spp. and stage A juvenile of *Rimicaris exoculata*; (B) same, rostral carapace length including rostral lobe used for juveniles and adults of *Rimicaris* spp.; (C) second segment of antennular peduncle; (D), third pereopod, lateral view. CL, carapace length; L, length; W, width.

posterior margin of the orbit to the midpoint of the posterodorsal margin. For the stage C juvenile, subadults, and adults of *Rimicaris* species, in which the rostrum is greatly reduced, the rostral carapace length (RCL), measured from the midpoint of the rostral lobe to the midpoint of the posterodorsal margin, is given. 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.

Differences between species within respective genus are so slight that a brief diagnosis is given for each species. Descriptive terminology for the mouthparts follows that of Komai and Segonzac (2003).

In respective synonymy, only taxonomic or systematic references are included.

#### SYSTEMATICS

##### *Family Alvinocarididae; Genus Rimicaris Williams and Rona 1986*

*Rimicaris* Williams and Rona 1986: 447 (in part); Martin and Hessler 1990: 8; Holthuis, 1993; Martin and Haney 2005: 467; *Iorania* Vereshchaka, 1996a: 952.

##### Type Species

*Rimicaris exoculata* Williams and Rona 1986.

**Description of Adult**

Body integument pitted with scattered, shallow punctations. Carapace (Fig. 2A, see 8A Later) ovate-oblong, distinctly broader than pleon with strongly inflated branchial regions; rostrum (Fig. 2C, see 8C see later) reduced to broadly rounded lobe fitting closely to posterior concavity of transverse ocular plate; dorsal surface of carapace generally rounded, obsolescent

epigastric ridge present, defined by conspicuous grooves extending from bases of antennal lobes; antennal lobes broadly rounded; branchiostegites strongly inflated; pterygostomial expansion covering greater part of antennal basicerite; ventral margin closely approximating bases of pereopods (Fig. 3).

Third pleonal pleuron unarmed marginally, posterolateral angle subrectangular; fourth and fifth pleura (Figs. 2D, 8D)

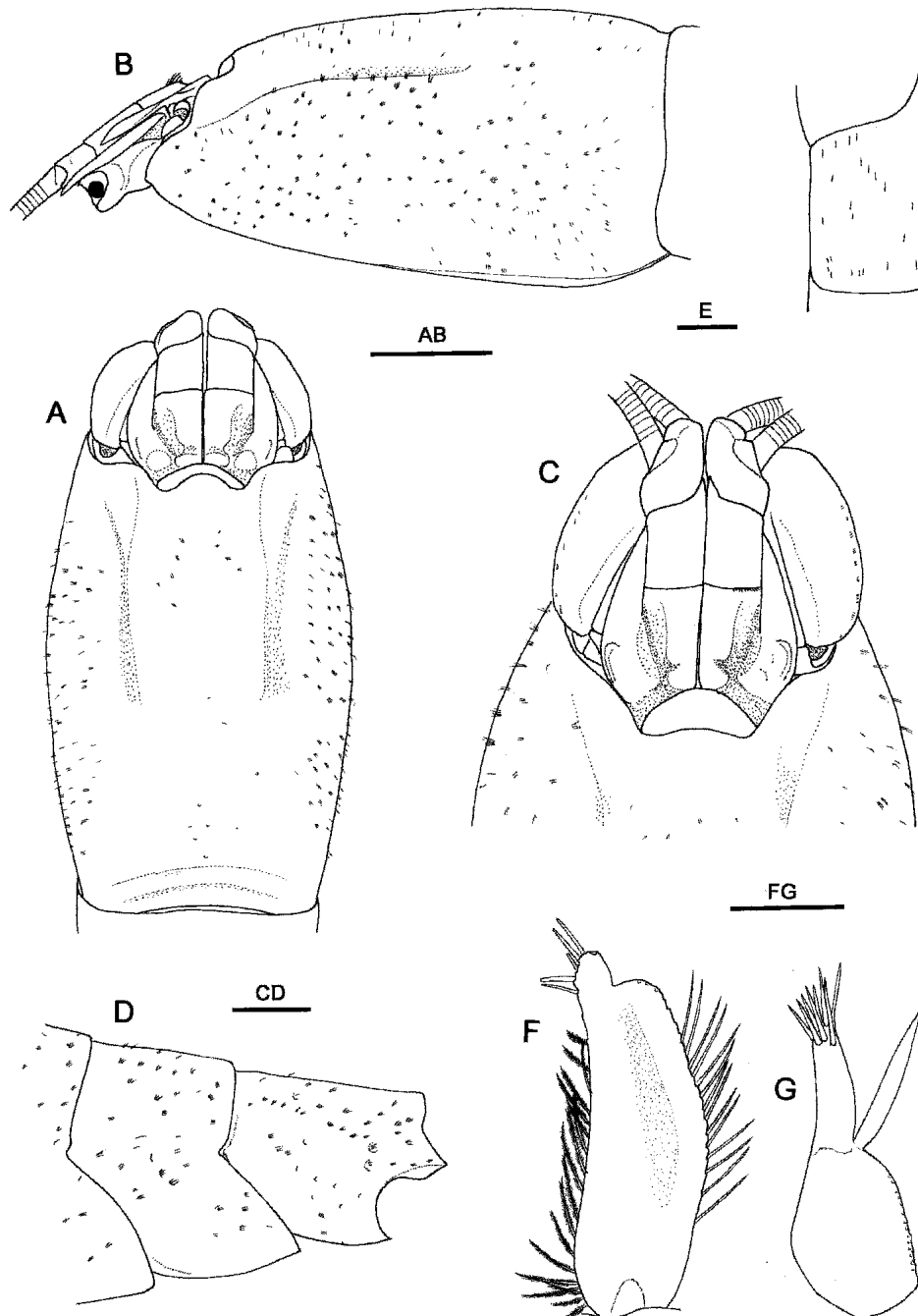


Figure 2. *Rimicaris exoculata* Williams & Rona, 1986. Adults. (A) Male (RCL 18.0 mm), MNHN-Na, Logatchev, Mid-Atlantic Ridge; (B-G) male (RCL 18.0 mm), CBM-ZC 6446, Rainbow, Mid-Atlantic Ridge. (A) Carapace and cephalic appendages, dorsal view; (B) same, lateral view; (C) anterior part of carapace and cephalic appendages, anterodorsal view; (D) fifth and sixth pleonal somites, lateral view; (E) second segment of left antennular peduncle, anterodorsal view; (F) endopod of left first pleopod, ventral view; (G) appendices interna and masculina of left second pleopod, mesial view. Scale bars: 5 mm for A, B; 2 mm for C, D; 1 mm for E-G.



**Remarks**

Two morphologically very similar species are known in *Rimicaris*. Autapomorphies of the genus include: the strongly modified ocular plate and anterior part of the carapace, the strongly inflated anterolateral part of the carapace, the operculiform antennae, and the presence of a mat of dense spinules on the flexor surfaces of the propodi of the third to fifth pereopods. Other unique characters among alvinocaridids include the secondary lack of the proximolateral tubercle of the first segment of the antennular peduncle, the unarmed distomesial angle of the first segment of the antennular peduncle, the stylocerite closely approximated to the antennular peduncle, the complete lack of the grooming apparatus on the carpus of the first pereopod and the possession of the functional appendix interna on the fourth pereopod.

Preliminary comparison of a partial sequence of mtCOI gene by Van Dover et al. (2001) suggested that the genetic diversity between the two species was low. Nevertheless, our study has confirmed that the two taxa can be distinguished morphologically, as discussed later.

The loss of the grooming apparatus of the first pereopods during the juvenile stages is highly remarkable. The functional change of this appendage is probably related to the diet change from food items from the surface of the habitat substrates to bacterial colonies developed on the scaphognathite of the maxilla and the caridean lobe of the first maxilliped. Van Dover et al. (1988) reported that the first pereopod has a function of scraping and grazing of filamentous bacteria covering the scaphognathite of the maxilla and the caridean lobe of the first maxilliped in adults of *Rimicaris exoculata*. Segonzac et al. (1993) observed a notable reduction of the gut size in *R. exoculata* compared with other alvinocaridid species and suspected that the reduction of the gut is related to the peculiar diet of the species, exclusively depending on bacterial colony. In fact, filamentous bacteria are found in the gut contents (Zbinden & Cambon-Bonavita 2003, Durand et al. in prep.). *In situ* observations of adult shrimps, recorded at the Elan site of the Snake Pit during the DiversExpedition cruise, shows that the first and second pereopods are always inserted in the space formed by the inflated anterolateral part of the carapace. Similar condition is also seen in preserved specimens (Fig. 3).

Martin and Hessler (1990) described the third maxilliped of *Rimicaris exoculata* as four long segments and one or two fused, shorter, basal segments, but this is not correct. The structure of the third maxilliped of *Rimicaris* is fundamentally similar to that of other alvinocaridid species (Komai & Segonzac 2003, Komai & Segonzac 2004, Komai & Segonzac 2005). It consists of three long segments and coxa. The antepenultimate segment consists of fusion of three segments, (i.e., merus, ischium and basis). Watabe and Hashimoto (2002) gave only a diagrammatic figure of the third maxilliped of *R. kairei*; there was no mention of the segmentation of this appendage.

***Rimicaris exoculata* Williams and Rona 1986**

*Rimicaris exoculata* Williams and Rona 1986: 448, Figures 4, 5, 6, 7; Williams 1987: 105; Martin and Hessler 1990: 6, Figures 3h, 4; Vereshchaka 1996b: 576–578; Segonzac 1997: 195; Shank et al., 1998: 89 (Table 1); 1999: 247, Figure 2; Martin and Shank 2005: 184; Martin and Harney 2005: 469; Komai and Segonzac 2006: 428, Figures 1, 2; Komai et al., 2007.

*Rimicaris chacei* Williams and Rona 1986: 455 (part). See “Remarks.”

*Chorocaris* n. sp.—Van Dover, 1995: 259.

*Iorania concordia* Vereshchaka 1996a: 954, Figures 1–5; 1996b: 577; Shank et al. 1998: 89 (Table 1).

*Rimicaris aurantiaca* Martin, Signorovitch and Patel 1997: 400, Figures 1–5; Shank et al. 1998: 98 (Table 1).

**Type Material Examined**

Paratypes of *Rimicaris chacei*. **TAG**. NOAA VENTS Program: 26°08.3'N, 44°49.6'W, 3620–3650 m, August 3, 1985, five juveniles at stage B (PCL 8.4–9.2 mm), USNM 228454; one juvenile at stage B (PCL 9.0 mm), MNHN-Na 10,535.

Paratype of *Iorania concordia*. **TAG**. BRAVEX-94: stn 3415, 26°09'N, 44°50'W, 3,650 m, September 23, 1994, one juvenile at stage B (PCL 8.6 mm), MNHN-Na.

**Other Material Examined***Rainbow*

PICO (DSV *Nautila*): dive 1264, 36°13.81'N, 33°54.07'E, 2,285 m, 30 June 1998, slurp gun 4, one male (RCL 18.9 mm), three females (RCL 16.2 mm–20.4 mm), MNHN-Na 16579; same data, two males (RCL 18.0, 19.0 mm), one female (CL 19.9 mm), CBM-ZC 6446. EXOMAR (ROV *Victor 6000*): dive 255-06, 36°13.76'N, 33°54.17'W, 2,293 m, August 5, 2005, slurp gun 8, nine females (RCL 14.0 mm–19.9 mm), MNHN-Na 16580; same data, seven males (CL 14.6 mm–19.5 mm), MNHN-Na 16581; dive 256-07, 36°13.76'N, 33°54.17'W, 2,293 m, August 6, 2005, slurp gun 3, one male (RCL 21.0 mm), seven females (RCL 11.0–19.7 mm), MNHN-Na 16582; dive 257-08, 36°13.76'N, 33°54.16'W, 2,293 m, August 7, 2005, slurp gun 1-2-4, one male (RCL 12.0 mm), 14 subadults or females (RCL 9.2–19.6 mm), MNHN-Na 16583; dive 258-09, 36°13.76'N, 33°54.16'W, 2,293 m, August 8, 2005, slurp gun 3, one juvenile at stage B (RCL 8.6 mm), 18 subadults or females (RCL 9.0–13.5 mm), four males (RCL 10.5–12.3 mm), MNHN-Na 16,584. MOMARETO (ROV *Victor*): dive 291-08, 36°13.75'N, 33°54.17'W, 2,297 m, August 19, 2006, slurp gun 1, three females (RCL 18.0–18.3 mm), one male (RCL 19.6 mm), CBM-ZC 9388.

**TAG**

EXOMAR (ROV *Victor 6000*): dive 260-11, 26°08.22'N, 44°49.56'W, 3,632 m, August 13, 2005, slurp gun 3, one juvenile at stage A (PCL 5.2 mm), MNHN-Na; same data, 26 juveniles at stage B (PCL 7.4–9.6 mm), MNHN-Na 16586; same data, 11 juveniles at stage C (RCL 7.1–8.6 mm), MNHN-Na 16587; 18 subadults or females (RCL 8.0–16.3 mm), one male (RCL 15.7 mm), MNHN-Na 16585; same dive, slurp gun 4, five males (RCL 12.5–15.2 mm), 13 subadults or females (RCL 9.2–14.9 mm), three juveniles at stage B (PCL 8.0–9.4 mm), CBM-ZC 9389; dive 262-13, slurp gun 1, four males (RCL 13.6–15.0 mm), six females (RCL 14.0–15.3 mm), CBM-ZC 9390.

*Snake Pit*

MICROSMOKE (DSV *Nautila*): dive 01, site Elan, 23°22.20'N, 44°57.08'W, 3,500 m, November 14, 1995, one

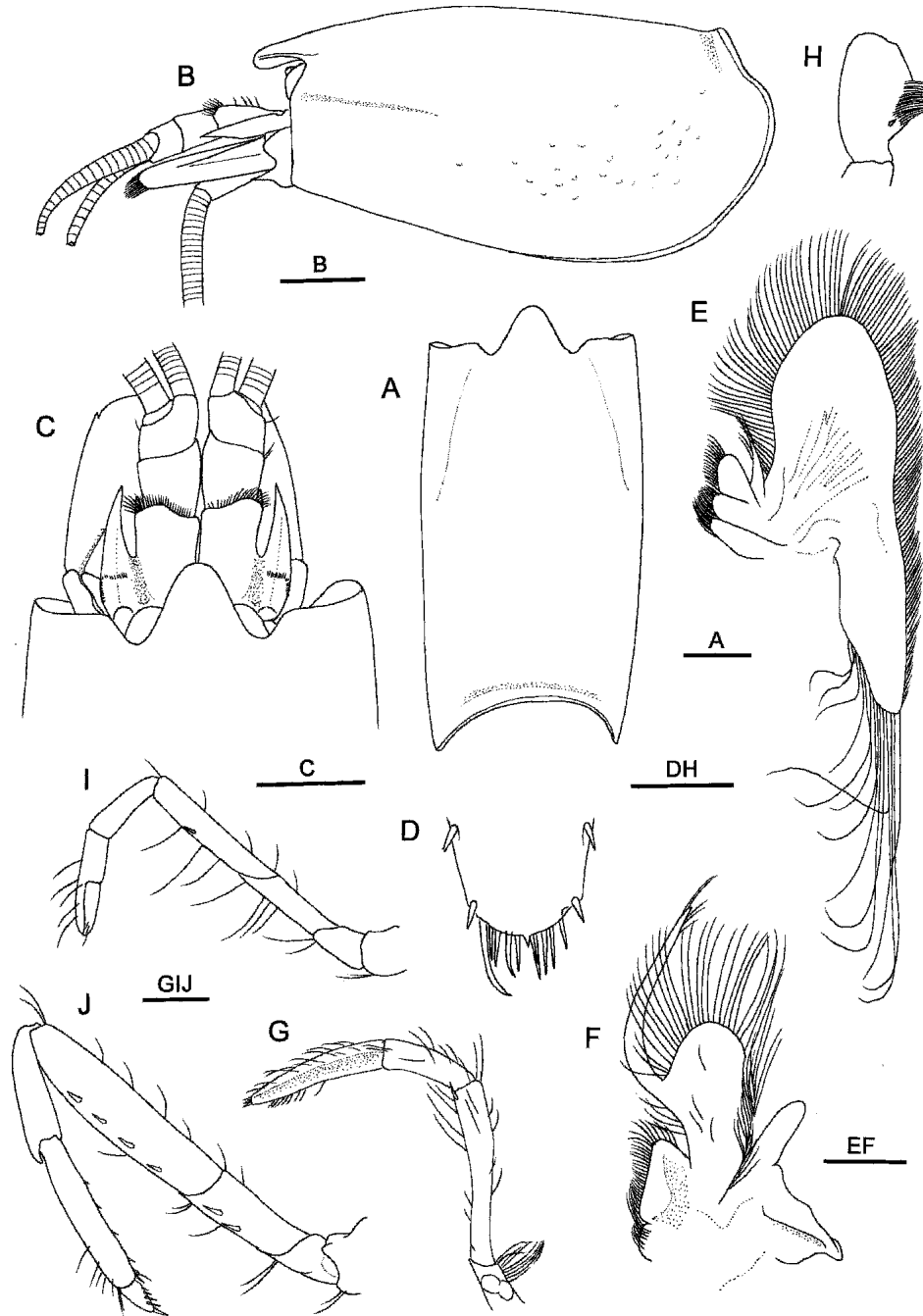


Figure 4. *Rimicaris exoculata* Williams & Rona, 1986. Juvenile at stage A (PCL 4.2 mm), MNHN-Na 16588, Snake Pit, Mid-Atlantic Ridge. (A) Carapace, dorsal view; (B) carapace and cephalic appendages, lateral view; (C) anterior part of carapace and cephalic appendages, dorsal view; (D) posterior part of telson, dorsal view; (E) left maxilla, ventral view; (F) left first maxilliped, ventral view; (G) left third maxilliped, lateral view; (H) carpus of left first pereopod, mesial view; (I) left second pereopod, lateral view; (J) left third pereopod, lateral view. Scale bars: 1 mm for A-C; 0.5 mm for D-J.

juvenile at stage B (PCL 7.3 mm), one juvenile at stage C (RCL 8.3 mm), four juveniles at stage D (RCL 8.6–8.8 mm), MNHN-Na; dive 02, site Ruches, 23°22.13'N, 44°57.13'W, 3,480 m, November 15, 1995, four males (RCL 18.1–19.1 mm), three females (RCL 10.6–18.5 mm), seven juveniles at stage B (PCL 7.0–9.0 mm), 12 juveniles at stage C (RCL 6.6–8.2 mm), nine subadults (RCL 7.5–9.0 mm), MNHN-Na. Divers-Expedition (DSV *Alvin*): dive 3672, 23°22.10'N, 44°56.91'W, 3,492 m, July 14, 2001, 77 juveniles at stage A (PCL 4.8–5.3

mm), one juvenile at stage B (PCL 8.4 mm), one juvenile at stage C (RCL 7.3 mm), two subadults (RCL 7.7, 8.9 mm), MNHN-Na 16588; same data, one male (RCL 16.3 mm), 13 subadults or adult females (RCL 8.0–13.0 mm), MNHN-Na.

#### Logatchev

DiversExpedition (DSV *Alvin*): dive 3668, 14°45.32'N, 44°58.79'W, 3028 m, 8 July 2001, 61 juveniles at stage B

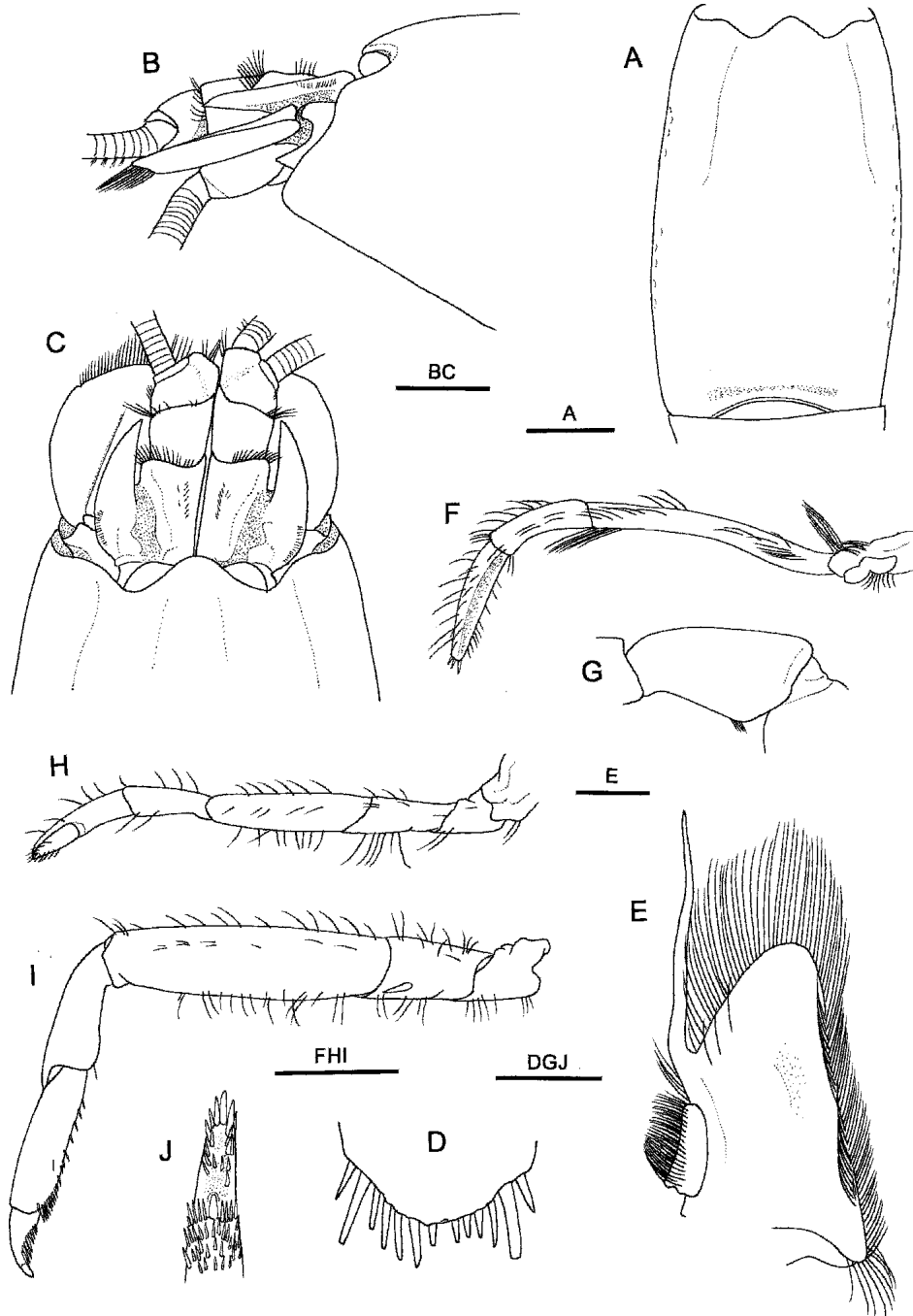


Figure 5. *Rimicaris exoculata* Williams & Rona, 1986. Juvenile at stage B (PCL 9.0 mm), MNHN-Na 16589, Logatchev, Mid-Atlantic Ridge. (A) Carapace, dorsal view; (B) anterior part of carapace and cephalic appendages, lateral view; (C) same, dorsal view; (D) posterior margin of telson, dorsal view; (E) left first maxilliped, ventral view; (F) left third maxilliped, lateral view; (G) carpus of left first pereopod, mesial view; (H) left second pereopod, lateral view; (I) left third pereopod, lateral view; (J) dactylus of left third pereopod, flexor view. Scale bars: 2 mm for A; 1 mm for B, C, F, H, I; 0.5 mm for D, E, G, J.

(PCL 7.4–9.1 mm), 59 juveniles at stage C (RCL 7.4–9.1 mm), 67 subadult or adult females (RCL 7.8–13.8 mm), 31 males (RCL 10.1–22.0 mm) MNHN-Na 16589. SERPENTINE (ROV *Victor 6000*): dive 315–06, Irina 2, 14°45.18'N, 44°58.74'W, 3,021 m, March 20, 2007, slurp gun 2, five juveniles at stage B (PCL 7.5–7.9 mm), six juveniles at stage C (RCL 7.9–9.5 mm), 16 subadults or adult females (RCL 8.5–

17.4 mm), three males (RCL 13.4–15.5 mm), MNHN-Na 16700; same data, five ovigerous females (RCL 15.2–18.4 mm), MNHN-Na 16701; same site, slurp gun 5, one juvenile at stage A (PCL 4.9 mm), MNHN-Na 16702; dive 316–07, same site, 14°45.17'N, 44°58.74'W, 3,022 m, slurp gun 4, 13 juveniles at stage A (PCL 4.4–5.0 mm), two juveniles at stage B (RCL 7.9, 8.2 mm), MNHN-Na 16703.

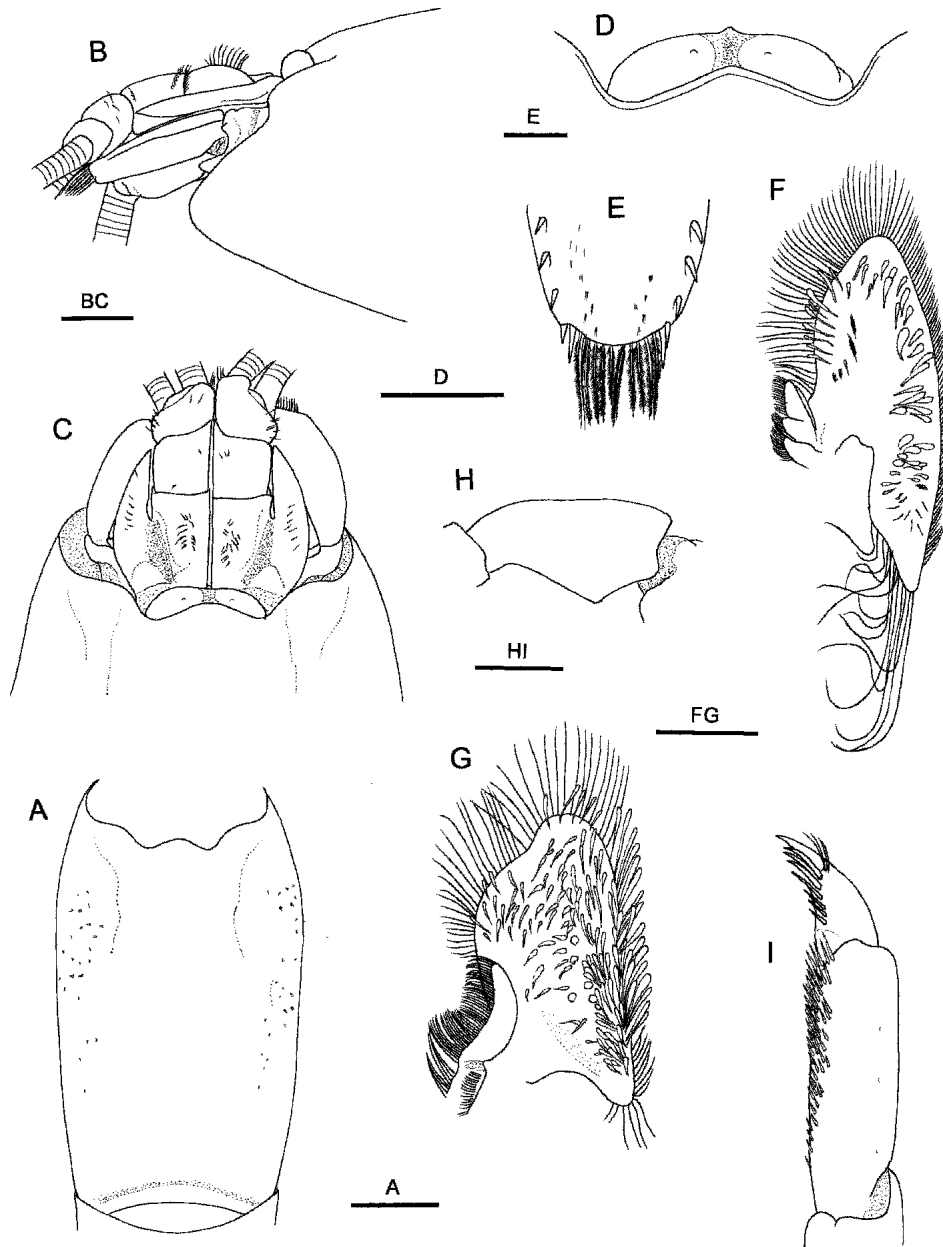


Figure 6. *Rimicaris exoculata* Williams & Rona, 1986. Juvenile at stage C (RCL 8.3 mm), MNHN-Na 16589, Logatchev, Mid-Atlantic Ridge. (A) Carapace, dorsal view; (B) anterior part of carapace and cephalic appendages, lateral view; (C) same, dorsal view; (D) fused eye-stalks, dorsal view; (E) posterior part of telson, dorsal view; (F) left maxilla, ventral view; (G) left first maxilliped, ventral view; (H) carpus of left first pereopod, mesial view; (I) dactylus and propodus of left third pereopod, lateral view. Scale bars: 2 mm for A; 1 mm for B-D, F, G; 0.5 mm for E, H, I.

#### Ashadze

SERPENTINE (ROV *Victor 6000*): dive 313-4, site Ashadze 1, marker SE1, 12°58.34'N, 44°51.77'W, 4,088 m, March 15, 2007, slurp gun 3, one juvenile at stage C (RCL 8.6 mm), MNHN-Na 16,699.

#### Mephisto

RV *Meteor*, M68/1 (ROV *Quest 4000*): stn 7, ROV-2, 04°47.834'S, 12°22.593'W, 3045 m, wall of hot smoker, May 11, 2006, one female (RCL 18.4 mm), one ovigerous female (RCL 19.4 mm), ZMH K-41458.

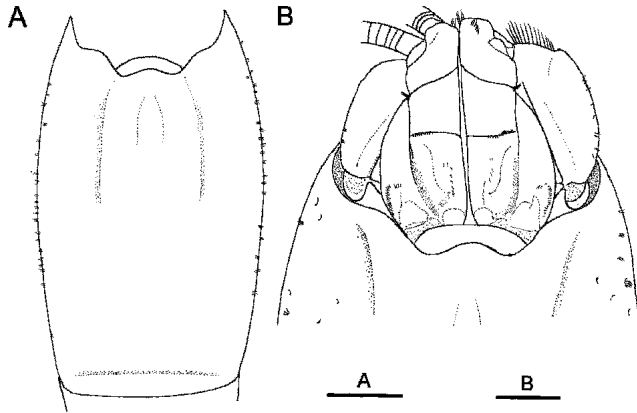
#### No collection data

Sixty females including subadults (RCL 8.3–20.4 mm), MNHN-Na 11872.

#### Diagnosis of Adult

Carapace and pleon with scattered tufts of short setae (Fig. 2A to D); anterolateral part strongly inflated but degree lesser extent to that of *R. kairei*. Antennular peduncle relatively stout; second segment (Fig. 2E) 1.21–1.59 times longer than wide (showing tendency toward increase of value with increase of body size).





**Figure 7.** *Rimicaris exoculata* Williams & Rona, 1986. Subadult (RCL 8.9 mm), MNHN-Na 16588, Snake Pit, Mid-Atlantic Ridge. (A) Carapace and ocular plate, dorsal view; (B) anterior part of carapace and cephalic appendages, anterodorsal view. Scale bars: 2 mm for A; 1 mm for B.

### Description

See Williams and Rona (1986) for adults; see Vereshchaka (1996a) and Martin et al. (1997) for juvenile of the stage B (see below).

### Ontogenetic Change in Postlarval Stages

Examination of the abundant material of postlarval stages, covering a wide range of size, has shown that *Rimicaris exoculata* exhibits dramatic morphological change at size of 7.0–9.0 mm in carapace length as seen by Shank et al. (1998). The smallest male specimen determined by the pleopod morphology is 10.1 mm in the orbital carapace length. For convenience, four stages are categorized for those juveniles based on morphological characters. Features of each stage are summarized as follows.

**Stage A** (Fig. 3). CL 4.8–5.3 mm. Rostrum (Fig. 4A, C) bluntly triangular in dorsal view, reaching nearly to midlength of first segment of antennular peduncle; dorsal surface convex, unarmed; lateral carina extending to orbital margin; ventral surface convex. Carapace (Fig. 4A, B) without epigastric ridge; antennal lobe obsolete; pterygostomial angle only slightly produced, rounded or slightly angular; postantennal groove shallow; branchiostegite not inflated; surface devoid of tufts of setae. Telson with five or six dorsolateral spines arranged in straight row; posterior margin (Fig. 4D) fringed with row of slender spines. Eye-stalks (Fig. 4B, C) fused mesially, with small papilla-like tubercle on anterior surface medially; cornea reduced, not faceted, but still recognizable; dorsal eyes extending posterior to about anterior 0.20 of carapace. Antennular peduncles (Fig. 4B, C) stout, but not closely approximated; first segment with small distolateral tooth partially obscured by setae on distal margin of segment; stylocerite reaching midlength of second segment, clearly separated by first segment by moderately narrow hiatus, lateral margin slightly convex. Antennal scale (Fig. 4C) not tightly fitting against antennular peduncle, with small, subacute distolateral tooth far exceeded by broadly rounded distal lamella; basicerite (Fig. 4B) with acute ventrodistal lateral tooth, not covered by pterygostomial projection of carapace. Maxilla (Fig. 4E) similar to that of adult

in general shape, but surfaces naked. First maxilliped (Fig. 4F) with caridean lobe moderately expanded, surfaces with few, weakly plumose setae; exopodal flagellum long. Second maxilliped moderately stout, not heavily setose; merus and ischium straight. Third maxilliped (Fig. 4G) with ultimate and penultimate segment combined longer than antepenultimate segment; antepenultimate with slender spine at ventrolateral distal angle. First pereopod with carpus (Fig. 4H) nearly as long as high; mesial face with grooming apparatus ventrally, consisting of small spine and patch of stiff setae. Second pereopod (Fig. 4I) with small spine on lateral surface ventrally; ischium unarmed. Third to fifth pereopods (Fig. 4J) diminishing slightly in length toward posterior; dactyli each with two rows of accessory spinules on flexor surface; propodi each with two rows of sparse spinules on flexor surface; meri each with three or four spines on lateral surface ventrally; ischia each with one or two spines on lateral surface ventrally. Appendices internae on second and third pereopods rudimentary buds, those of fourth and fifth pleopods fully developed, with terminal cluster of cincinnuli.

**Stage B** (Fig. 5). CL 7.0–9.5 mm. Rostrum (Fig. 5A, C) rounded, reaching tip of antennal lobe; ventral surface slightly convex or flat. Carapace (Fig. 5A to C) with scattered tufts of very short setae or single setae on surface; noticeably produced pterygostomial lobe partially covering antennal basicerite, but otherwise similar to that of stage A. Telson with seven to nine dorsolateral spines arranged in faintly sinuous row; posterior margin (Fig. 5D) fringed with slender spinules. Eye-stalks (Fig. 5C) generally similar to those of stage A, but papilla-like tubercles on anterior surface of corneal region reduced. Antennular peduncles (Fig. 5B, C) becoming stouter and more closely approximated; first segment with distolateral tooth greatly reduced to tiny projection and with distinct distomesial tooth; stylocerite reaching distal margin of second segment, still narrowly separated from first segment, lateral margin noticeably convex. Antennal scale (Fig. 5C) becoming broader, but still not tightly fitting against antennular peduncle, with trace of distolateral tooth; basicerite (Fig. 5B) partially covered by pterygostomial projection of carapace. Maxilla similar to that of stage A. First maxilliped (Fig. 5E) with broad caridean lobe, but facial plumose setae few, restricted to adjacent to margins; exopodal flagellum still developed, reaching or distinctly overreaching anterior margin of caridean lobe. Second maxilliped becoming more slender and more setose. Third maxilliped (Fig. 5F) with distal two segments combined distinctly shorter than antepenultimate segment; slender spine at ventrodistal lateral angle of antepenultimate segment missing. First pereopod with carpus (Fig. 5G) being longer than high, with small tuft of short setae on ventral margin, representing rudiment of grooming apparatus. Second pereopod (Fig. 5H) unarmed on merus. Third pereopod (Fig. 5I) with more than two rows of accessory spinules on flexor surface of dactylus (Fig. 5J); propodus becoming shorter proportionally, with mat of dense spinules extending to midlength of flexor surface, followed by two rows of spinules in proximal half; merus unarmed or one or two spines; ischium with one or two spines. Fourth and fifth pereopods with less spinose flexor surfaces of propodi; each merus unarmed or armed with one to four spines on lateral surface; ischium unarmed or armed with one or two spines on lateral surface. Appendices internae on second and third pereopods short and slender, lacking cincinnuli; those on fourth and fifth pereopods stout, functional.

Stage C (Fig. 6). CL 6.6–8.2 mm. Rostrum (Fig. 6C, D) reduced to broadly rounded rostral lobe. Carapace (Fig. 6A to C) with pterygostomial angle strongly produced anteriorly, rounded; branchiostegite weakly inflated. Telson with seven to nine dorsolateral spines arranged in sinuous row; posterior margin (Fig. 6E) fringed with row of plumose setae. Eye-stalks (Fig. 6D) broadly fused mesially but with trace of median notch on anterior surface; separation of cornea and eye-stalk unclear; no papilla-like tubercle on eye-stalk. Antennular peduncles (Fig. 6B, C) stout, closely approximated as in adult; first segment unarmed on distolateral and distomesial angles; stylocerite closely appressed to antennular peduncle, lateral margin strongly convex. Antennal scale (Fig. 6B, C) tightly fitting against antennular peduncle, without distolateral tooth but with short transverse groove distolaterally; basicerite partially covered by pterygostomial projection of carapace. Maxilla (Fig. 6F) with numerous plumose setae-like structure formed by bacteria on surfaces of scaphognathite. First maxilliped (Fig. 6E) with or without trace of flagellum of exopod; caridean lobe broad, with numerous heavily plumose setae on surfaces. Second maxilliped with merus and ischium slightly curved. Carpus of first pereopod (Fig. 6H) without trace of grooming apparatus. Other appendages as in previous stage.

Stage D, or subadults (Fig. 7). CL 7.5 mm or more. Generally similar to adults (see “Diagnosis” of the genus), but inflation of carapace still weaker than adults (Fig. 7A). Ocular plate completely formed, fused with anterodorsal part of carapace (Fig. 7B).

#### Size

Ovigerous females RCL 15.2–19.4 mm; males RCL 10.6–22.0 mm. The largest specimen is the male RCL 22.0 mm, TL about 70 mm.

#### Distribution

Mid-Atlantic Ridge, hydrothermal vent fields at Rainbow, Lucky Strike, TAG, Snake Pit, Broken Spur, Logatchev, Ashadze, and Mephisto sites, 1,700–4,088 m. The specimen from Ashadze 1 site extends the bathymetric range of the species to 4,088 m.

#### Remarks

Adult specimens from TAG, Rainbow, Snake Pit, Logatchev, Ashadze and Mephisto vent sites were available for study. The specimens are generally similar, and there is little doubt that they represent a single species. In fact, based on allozyme data, Creasey et al. (1996) showed that the genetic variation in the populations from TAG and Broken Spur was low. Vereshchaka (1997b) reported statistically significant divergence between two populations within the TAG vent field, but we could not find any morphological differences of species level significance.

As shown earlier, the juveniles can be categorized in four sequential stages. It is remarkable that there is no significant increase of size during molts from the stage B to stage D. It can be assumed that the shrimp spends much energy for great morphological change rather than increase of body size. The most notable change is seen in the structure of the anterior part of the carapace, eye-stalks and antennae. Also, the reduction of the exopod on the first maxilliped and the loss of the grooming apparatus on the carpus of the first pereopod are also remark-

able. The loss of the spination on the second to fifth pereopods is here documented for the first time. Most of the structures are completed at the stage D (subadult).

Shank et al. (1998, 1999) showed that *Iorania concordia* and *Rimicaris aurantiaca* were described from juvenile stage of *R. exoculata* based on studies of allozyme and mtDNA. Our study confirms the conclusion of Shank et al. (1998, 1999). Reexamination of the type material of *I. concordia* and *R. aurantiaca* (one paratype was available for *I. concordia*; the holotype and paratypes were available for *R. aurantiaca*) has shown that all specimens of the two nominal taxa correspond to the stage B juvenile of *R. exoculata*. The paratype of *I. concordia* (MNHN-Na) seems to be just before molting, with the rostral margin of the next molt is visible throughout the integument. The visible rostral margin of the next molt is less produced as illustrated and is similar to the configuration of the rostral margin in the stage C. This provides further evidence that the stages categorized here can be aligned in an ontogenetic sequence.

Juveniles of the stages A and B of *Rimicaris exoculata* are similar to juveniles of *Chorocaris chacei* of similar sizes. The two species occur sympatrically, and it is easy to confuse them without careful observation. In fact, some paratypes of *C. chacei* are actually *R. exoculata*. Throughout the juvenile stages, *Rimicaris exoculata* is distinguishable from *C. chacei* by the less developed distolateral tooth of the first segment of the antennular peduncle. In the stage A juvenile, the distolateral tooth is small, and partially obscured by setae on the dorsodistal margin of the first peduncular segment; in the stage B juvenile, the tooth is missing. In *C. chacei*, the distolateral tooth is always conspicuous, reaching to the midlength of the second peduncular segment (Fig. 11A, see later). Furthermore, the stage A juveniles of *R. exoculata* is distinguishable from juveniles of *C. chacei* by the more strongly produced rostrum (cf. Fig. 4A and Fig. 11A), the presence of spiniform setae on the posterior margin of the telson (Fig. 4D), and the meri of the second and third pereopod being armed with lateral spine(s) (Fig. 4J). In juveniles of *C. chacei*, the posterior margin of the telson bears plumose setae mesial to the two posterolateral pairs of spines (Fig. 11C), instead of spiniform setae; and the meri of the second and third pereopod are unarmed (Fig. 10E). The stage B juveniles of *R. exoculata* differ from juveniles of *C. chacei* in the relatively broader rostrum and the lack of a grooming apparatus on the carpus of the first pereopod. *Chorocaris chacei* has a well-developed grooming apparatus on the carpus of the first pereopod throughout the postlarval stage to adult.

#### *Rimicaris kairei* Watabe and Hashimoto 2002 (Fig. 8)

*Rimicaris* aff. *exoculata*—Van Dover et al. 2001: 820, Figure 2A, B, G.

*Rimicaris kairei* Watabe and Hashimoto 2002: 1168, Figures 1 to 4; Martin and Shank 2005: 184; Martin and Haney 2005: 469; Hashimoto 2006: 429, Figures 1, 2.

#### Material Examined

DSV *Shinkai 6500*: dive 659, Kairei Field, Rodriguez Triple Junction, Central Indian Ridge, 25°19.22'S, 70°02.39'E, 2,415–2,460 m, February 15, 2002, 3 males (RCL 12.1–20.8 mm), 7 nonovigerous females (RCL 12.5–22.9 mm), JAMSTEC

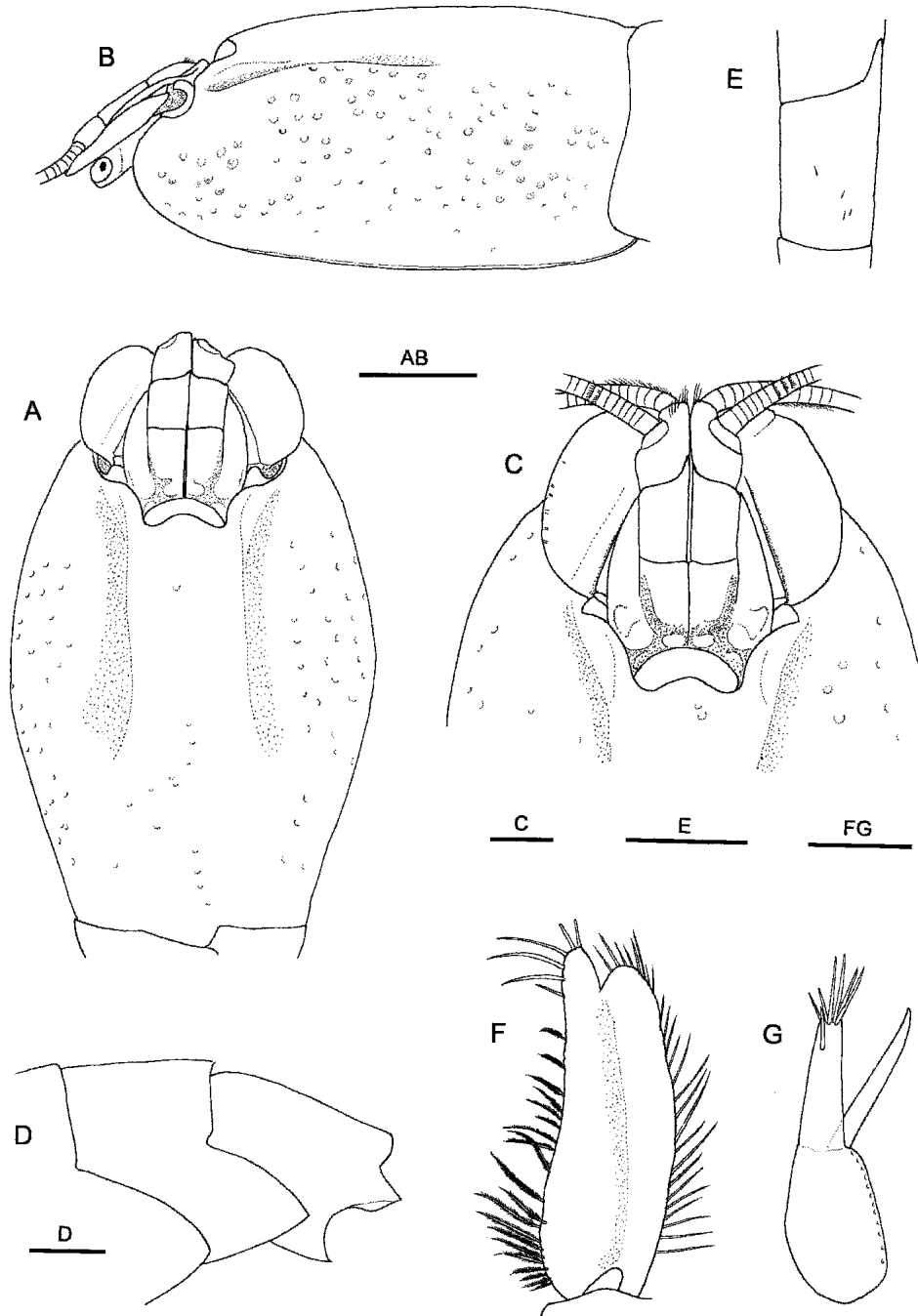


Figure 8. *Rimicaris kaiei* Watabe & Hashimoto, 2002. A to E, female (RCL 17.4 mm), JAMSTEC 047496, Kairei Field, Central Indian Ridge; F, G, male (RCL 20.5 mm), same lot. (A) Carapace and cephalic appendages, dorsal view; (B) same, lateral view; (C) anterior part of carapace and cephalic appendages, anterodorsal view; (D) fifth and sixth pleonal somites, lateral view; (E) second segment of left antennular peduncle, anterodorsal view; (F) endopod of left first pleopod, ventral view; (G) appendices interna and masculina of left second pleopod, mesial view. Scale bars: 5 mm for A, B; 2 mm for C to E; 1 mm for F, G.

047496. ROV *Kaiko*: dive 168, same field, 25°19.16'S, 70°02.40'E, 2,452 m, August 26, 2000; 6 females (RCL 12.6–15.0 mm), JAMSTEC 032683–032851.

#### Diagnosis of Adult

Carapace and pleon completely naked on surface (Fig. 7A to D); anterior part of branchial region more strongly inflated than

in *R. exoculata* (Fig. 7A). Antennular peduncle relatively slender; second segment (Fig. 7E) 1.57–1.86 times longer than wide.

#### Description

See Watabe and Hashimoto (2002).

#### Size

Males RCL 12.1–20.8 mm. Largest specimen, a female, RCL 22.9 mm, TL ca. 73 mm.

**Distribution**

Known only from Kairei and Edmonds vent fields at the Rodriguez Triple Junction on the Central Indian Ridge, Indian Ocean, 2,415–3,320 m.

**Remarks**

Watabe and Hashimoto (2002) cited three morphological characters in differentiating *R. kairei* and *R. exoculata*; the presence or absence of tufts of short setae on the carapace and pleon (tufts of setae are absent in *R. kairei*, present in *R. exoculata*), the relative length of the antennal flagellum (longer in *R. kairei* than in *R. exoculata*), and the shape of the second to fifth pereopods (the pereopods are more slender in *R. kairei* than in *R. exoculata*). Our study has shown that the latter two characters are not reliable, because the proportional values greatly overlap between *R. kairei* and *R. exoculata*, as summarized in Table 2. Even statistically, there are no significant differences between the mean values of the two species (the length of the antennal flagellum:  $t = 1.5616$ , degree of freedom 18,  $P > 0.05$ ; the proportion of the merus of the third pereopod:  $t = 0.1098$ , degree of freedom 34,  $P > 0.05$ ). Only two specimens of *R. exoculata* were available to Watabe and Hashimoto (2002), and therefore, it is obvious that their evaluation of intraspecific variation was inadequate. Nevertheless, the first character is still reliable in distinguishing the two species throughout subadult to adult stages. Additionally, the antennular peduncle is less stout in *R. kairei* than in *R. exoculata*. The proportion of the second segment is used as an indicator. The second segment is 1.57 to 1.86 times longer than wide in *R. kairei*, 1.21 to 1.59 in *R. exoculata*. The branchial region of the carapace seems to be more strongly inflated in *R. kairei* than in *R. exoculata* (Fig. 2A and Fig. 8A).

During this study, no juvenile specimens have been available to us, but we suspect that *R. kairei* also has dramatic ontogenetic change in early postlarval stage as in *R. exoculata*.

**Genus *Chorocaris* Martin and Hessler 1990**

*Rimicaris* Williams and Rona 1986: 447 (in part).

*Chorocaris* Martin and Hessler 1990: 2 (in part); Holthuis 1993: 72; Martin and Haney 2005: 463.

TABLE 2.

**Variation in the length of the antennal flagellum and the proportion of the merus of the third pereopod in two *Rimicaris* species. Abbreviations: AFL, length of antennal flagellum; CL, carapace length; ML, length of merus; MW, width of merus; P3, third pereopod.**

	AFL/CL	P3 ML/MW
<i>Rimicaris exoculata</i>		
Male	1.59–2.44 ( $n = 6$ )	3.90–4.86 ( $n = 10$ )
Female	1.23–2.17 ( $n = 4$ )	4.39–4.69 ( $n = 11$ )
<i>Rimicaris kairei</i>		
Male	1.64 ( $n = 1$ )	4.27–4.41 ( $n = 2$ )
Female	1.20–1.88 ( $n = 7$ )	4.14–4.67 ( $n = 14$ )

**Description**

Body integument pitted with scattered, very shallow punctations or nearly smooth. Rostrum broadly rounded or bluntly triangular, reaching or slightly overreaching anterior margins of broadly fused eye-stalks; dorsal surface rounded, unarmed; ventral surface convex or flat. Carapace nearly as broad as pleon; dorsal surface rounded; antennal tooth weak, blunt or showing as broadly rounded lobe; anterolateral part only slightly inflated; pterygostomial expansion at most partially covering antennal basicerite; ventral margin not closely approximating bases of pereopods.

Third pleonal pleuron unarmed marginally, posterolateral angle rounded; fourth and fifth pleura each with blunt or subacute posteroventral angle, without marginal teeth or denticles. Telson broad, slightly narrowed posteriorly; posterior margin broadly convex, with two or three pairs of small spines at lateral angles and row of numerous moderately long plumose setae; six to nine dorsolateral spines arranged in sinuous row.

Eye-stalks broadly fused mesially; no conspicuous tubercles on anterior surface. Antennae normal in structure. Antennular peduncles stout, somewhat depressed dorsoventrally, not closely approximated, thus mesial face rounded; first segment with strong distolateral and small distomesial teeth; dorsal surface convex, groove separating stylocerite deep; stylocerite moderately slender, clearly separated from first segment, reaching or overreaching midlength of second segment, its lateral margin slightly convex; proximolateral tubercle prominent; second segment nearly as long as broad to slightly longer than broad, with small distomesial tooth. Antennal scale generally oval with distal margin broadly rounded, blunt distolateral tooth present; short transverse suture extending mesially from base of distolateral tooth; dorsal surface with prominent mid-dorsal carina; basicerite with subacute ventrolateral tooth.

Mandible and maxillule typical of family. Maxilla and first maxilliped with numerous plumose seta-like structures on ventral surfaces in *C. chacei*, without such seta-like structures in *C. vandoverae* and *C. paulexa*; posterior lobe of scaphognathite somewhat elongate; caridean lobe of first maxilliped broad, lacking flagellum. Second maxilliped consisting of six segments as in other alvinocaridids; merus and ischium-basis fused segments moderately stout, nearly straight, with numerous heavily plumose setae on lateral margins; epipod large, subsemicircular, with rudimentary podobranch. Third maxilliped consisting of four segments; ultimate segment stout, 1.2–1.3 times longer than penultimate segment, tapering distally, with some spines distally; lateral surface of ultimate segment longitudinally carinate, with row of stiff setae; cross section trigonal; antepenultimate segment flattened dorsoventrally, with numerous heavily plumose setae on margins and with prominent cluster of long setulose setae on low elevation at proximomesial part; coxa with large, bilobed epipod; no strap-like process on epipod.

First pereopod typical of family, polymorphic; carpus with obliquely truncate distal margin to accommodate proximal part of palm, mesial face with grooming apparatus consisting of patch of stiff setae and one or two spinules (Fig. 9E). Second pereopod moderately slender; chela slightly longer than carpus; merus and ischium unarmed. Third to fifth pereopods moderately stout, similar in structure but slightly increasing in relative length from third to fifth; dactyli subconical, 0.3–0.4 length of

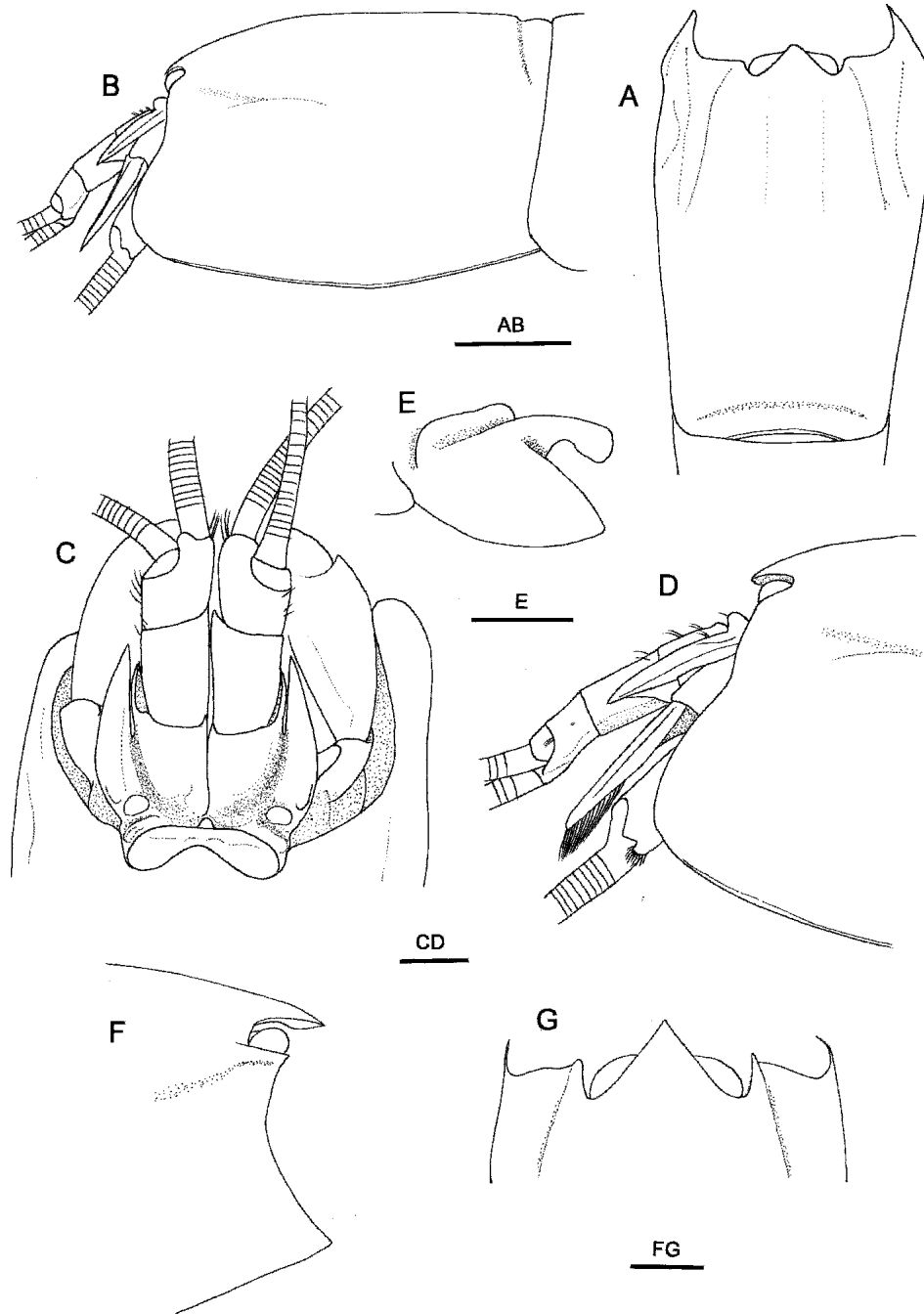


Figure 9. *Chorocaris chacei* (Williams & Rona 1986). (A to D) Ovigerous female (PCL 16.5 mm), MNHN-Na 16568, Lucky Strike, Mid-Atlantic Ridge; (E) female (PCL 21.5 mm), CBM-ZC 9391, same locality; (F, G) male (PCL 15.3 mm), CBM-ZC 9392, same locality. (A) Carapace and eye stalks, dorsal view; (B) carapace and cephalic appendages, lateral view; (C) anterior part of carapace and cephalic appendages, anterodorsal view; (D) same, lateral view; (E) protopod of left uropod, dorsolateral view; (F) anterior part of carapace and ocular appendage, lateral view; (G) same, dorsal view. Scale bars: 5 mm for A, B; 2 mm for C, D, F, G; 1 mm for E.

propodi, each terminating in strong, curved corneous unguis, flexor surface with about ten corneous, distally curved, spinules arranged in three or four rows; propodi increasing in length from third to fifth, each with three or four spinules on ventrodistal margin and irregular two rows of spinules on ventral surface in third and fourth, with double row of spinules laterally and single row of sparse spinules mesially in fifth; carpi 0.7–0.9 length of propodi in third and fourth pereopods, 0.5–0.6

in fifth pereopod; meri and ischia unarmed. No strap-like epipods on pereopods. Gill formula typical of family (Table 1).

Endopod of first pleopod sexually dimorphic; in male, endopod (Figs. 9F, 10D) terminating in two greatly unequal lobes, mesial lobe much produced, with four or five long spiniform setae directed mesially; in female, endopod simple. Second pleopod with slender appendix interna, lacking cincinuli (Figs. 9G, 10E); appendix masculina slightly shorter than

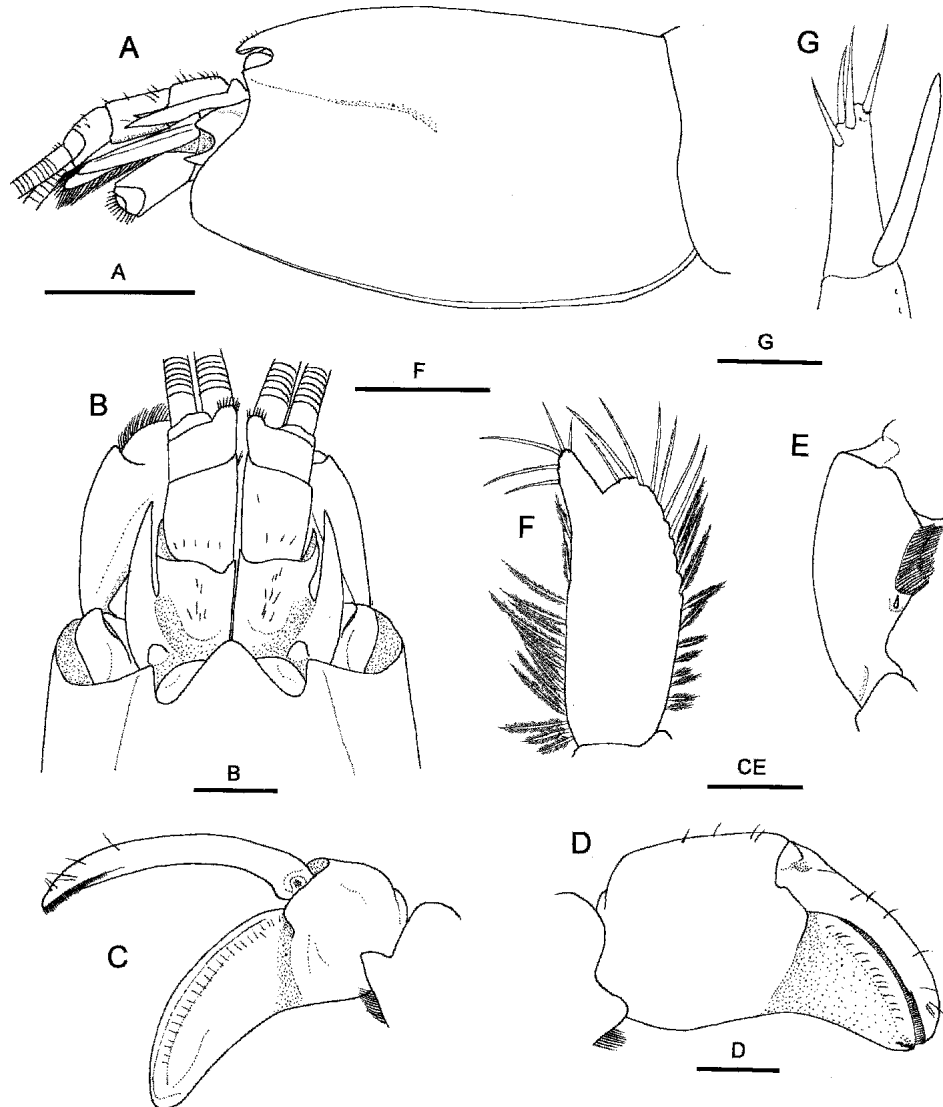


Figure 10. *Chorocaris chacei* (Williams & Rona, 1986). (A, B, C, E) Female (PCL 13.2 mm), MNHN-Na 16571, Lucky Strike, Mid-Atlantic Ridge; (D) holotype, female (cl 17.9 mm), USNM 228452, TAG, MidAtlantic Ridge; (F, G) male (cl 11.5 mm), MNHN-Na, Lucky Strike, Mid-Atlantic Ridge. (A) Carapace and cephalic appendages, dorsal view; (B) anterior part of carapace and cephalic appendages, dorsal view; (C) chela of right first pereopod, inner view; (D) chela of left first pereopod, inner view; (E) carpus of left first pereopod, mesial view; (F) endopod of left first pleopod, ventral view; (G) appendices interna and masculina of left second pleopod, mesial view. Scale bars: 5 mm for A; 2 mm for B; 1 mm for C, D-F; 0.5 mm for G.

appendix interna, tapering distally, with several spiniform setae. Third and fourth pleopods each with slender appendix interna lacking cincinnuli. Fifth pleopods with normally developed, functional appendix interna, bearing cincinnuli.

Uropod with broad rami; exopod with two small spines at posterolateral angle and with distinct transverse suture; posterolateral projection of protopod terminally blunt.

#### Composition

*Chorocaris chacei* (Williams and Rona, 1986); *C. vandoverae* Martin and Hessler 1990 (type species); and *C. paulexa* Martin and Shank 2005.

#### Geographical Range

Mid-Atlantic Ridge (between 23°N and 37°N), Mariana Back-Arc Basin in the northwestern Pacific and southern East Pacific Rise.

#### Remarks

Presumable synapomorphies among species of *Chorocaris* and *Rimicaris* are the following: the tendency of a rostral reduction, nonacuminate antennal tooth of the carapace, nonmarginally dentate posterolateral margin of pleura of fourth and fifth pleonal somites, the presence of a distolateral transverse suture on the antennal scale, and the nonacuminate uropodal protopod. Shank et al. (1999) suggested that *Chorocaris* is a paraphyletic assemblage with *C. chacei* being more closely related to *Rimicaris exoculata*. Consequently, we tried to identify synapomorphies of *C. chacei* and *R. exoculata*. It is interesting to note that the specimens of *C. chacei* in spawning molt have suboperculiform antennae, which are distinctly directed downward, like adults of *Rimicaris* species; the rostrum is reduced to a broadly rounded lobe, although the degree of the reduction is in a lesser extent than in *Rimicaris*. In the ovigerous specimens of *C. vandoverae* and *C. paulexa* the antennae are normal, only

slightly directed downward; the rostrum is short but still more distinct. Comparison with other alvinocaridid taxa clearly suggests that the possession of suboperculiform antennae and the reduction of the rostrum are apomorphic. Furthermore, ovigerous females of *C. chacei* lack shallow longitudinal depressions, ornamented with numerous longitudinal striae, on either side of the midline of the carapace, which are present in ovigerous females of *C. vandoverae* and *C. paulexa*. Species of *Rimicaris* also do not possess such depressions on the carapace in spawning females. In *C. vandoverae* and *C. paulexa*, the scaphognathite of the maxilla and the caridean lobe of the first maxilliped are nearly naked on the ventral surfaces, whereas in *C. chacei*, they are provided with numerous plumose seta-like structures on the surfaces, like *Rimicaris* species. The structure of the appendix masculina is also similar between *C. chacei* and *Rimicaris* species. The appendix masculina is armed with several spiniform setae distally in *C. chacei* and two *Rimicaris* species, but in *C. vandoverae*, a row of spiniform setae extends onto the dorsal surface of the appendix masculina. Male specimens of *C. paulexa* were not available for study. The observation seems to support the proximity between *C. chacei* and *Rimicaris* species. Nevertheless, in this study, we did not attempt to establish a new genus for *C. chacei*, because we believe that highly corroborated phylogeny is necessary for the establishment of a new higher taxon for such a specific taxon with morphologically similar species. Furthermore, we could not identify single, stable character for discrimination. Most of the characters above cited are affected by ontogeny or sex. For the time being, *Chorocaris* should be considered as a possible paraphyletic taxon.

Differentiation between *Chorocaris* and *Opaepele* Williams and Dobbs 1995 now appears rather delicate (Komai et al., 2007). Nevertheless, *Opaepele* can be distinguished from *Chorocaris* by the acuminate antennal and pterygostomial teeth of the carapace, the denticulate posterolateral margin of the fifth pleonal pleuron, the well differentiated, sharp distolateral tooth of the antennal scale and the sharply pointed posterolateral projection of the uropodal protopod. *Mirocaris* superficially resembles *Chorocaris*, but the presence of strap-like epipods immediately distinguishes *Mirocaris* from *Chorocaris*. In the MidAtlantic Ridge, species of the two genera are often found sympatrically, and it is advisable to check the presence or absence of pereopodal epipods for accurate identification.

Unidentified specimens provisionally assigned to *Chorocaris* have been reported (Martin & Haney 2005). Desbruyères et al. (1994) noted the possibility of existence of *Chorocaris* species in material from Lau and North Fiji Basin, but since then no specimens referable to *Chorocaris* have been collected from these localities. Van Dover et al. (2001) recorded *Chorocaris* sp. from Kairei Field, Central Indian Ridge, but the occurrence of species of *Chorocaris* in the vent fields on the Central Indian Ridges has not been confirmed. Komai et al. (2006) indicated that *Chorocaris* sp. of Van Dover et al. (2001) might be identical with *Mirocaris indica* Komai, Martin, Zala, Tsuchida and Hashimoto 2006, a species described from Kairei and Edmond vent fields, because of its superficial resemblance to species of *Chorocaris*. A few specimens of a shrimp species that appear to belong to *Chorocaris* have been found on seamounts of the Kermadec Ridge off New Zealand (Webber, 2004). This record also needs to be verified.

Species of *Chorocaris* are distinguished by subtle morphological differences, some of which are growth-related. There-

fore, in the following key, different stages or sexes of a same species are treated separately.

#### Key to Species of *Chorocaris* (Adult)

1. a. Carapace with shallow longitudinal depression on either side of dorsal midline ..... 2
- b. Carapace without shallow longitudinal depression on either side of dorsal midline ..... 3
2. a. Pterygostomial projection terminally blunt; rostrum relatively large; distolateral tooth of antennal scale blunt, closely approximated to lamella, thus apparently inconspicuous ..... *C. vandoverae* (spawning females)
- b. Pterygostomial projection subacutely pointed; rostrum relatively small; distolateral tooth of antennal scale subacute, clearly separated from lamella by V-shaped notch.. ..... *C. paulexa* (spawning females)
3. a. Antennal tooth of carapace broadly rounded..... *C. chacei* (spawning females)
- b. Antennal tooth of carapace blunt, but clearly delineated..... 4
4. a. Pterygostomial expansion subacutely pointed; distolateral tooth of antennal scale distinctly delineated..... *C. paulexa* (nonspawning females)
- b. Pterygostomial expansion rounded..... 5
5. a. Rostrum with nearly straight lateral margins; distolateral tooth of antennal scale small, but distinctly separated from lamella by V-shaped notch; plumose seta-like structures present on ventral surfaces of scaphognathite of maxilla and caridean lobe of first maxilliped; appendix masculina only with terminal or subterminal spines ..... *C. chacei* (males or nonspawning females)
- b. Rostrum with weakly convex lateral margins; distolateral tooth of antennal scale blunt, closely approximated to lamella; no plumose seta-like structures present on ventral surfaces of scaphognathite of maxilla and caridean lobe of first maxilliped; appendix masculina with terminal spines and rows of spines extending onto dorsal surface ..... *C. vandoverae* (males or nonspawning females)

#### *Chorocaris chacei* (Williams & Rona 1986 Figs. 9–11)

*Rimicaris chacei* Williams and Rona 1986: 455 (in part), Figures 5–7; Williams 1987: 105.

*Chorocaris chacei* – Martin and Hessler 1990: 2, 8, Figure 3f, g; Martin and Hessler 1990: 6, Figures 3h, 4; Segonzac et al. 1993: 540 and addendum (part); Vereshchaka 1996b: 577; Shank, in Desbruyères and Segonzac 1997: 195; Shank et al. 1998: 89 (Table 1); 1999: 246 (Table 1), 247 (Table 2), 249, Figure 2; Martin and Shank 2005: 184; Martin and Haney 2005: 464; Komai and Segonzac 2006: 421, Figures 1–5.

#### Type Material

Holotype. TAG. NOAA VENTS Program (RV *Researcher*): 26°08.3'N, 44°49.6'W, 3,620–3,650 m, August 3, 1985, dredge, female (PCL 18.3 mm), USNM 228452.

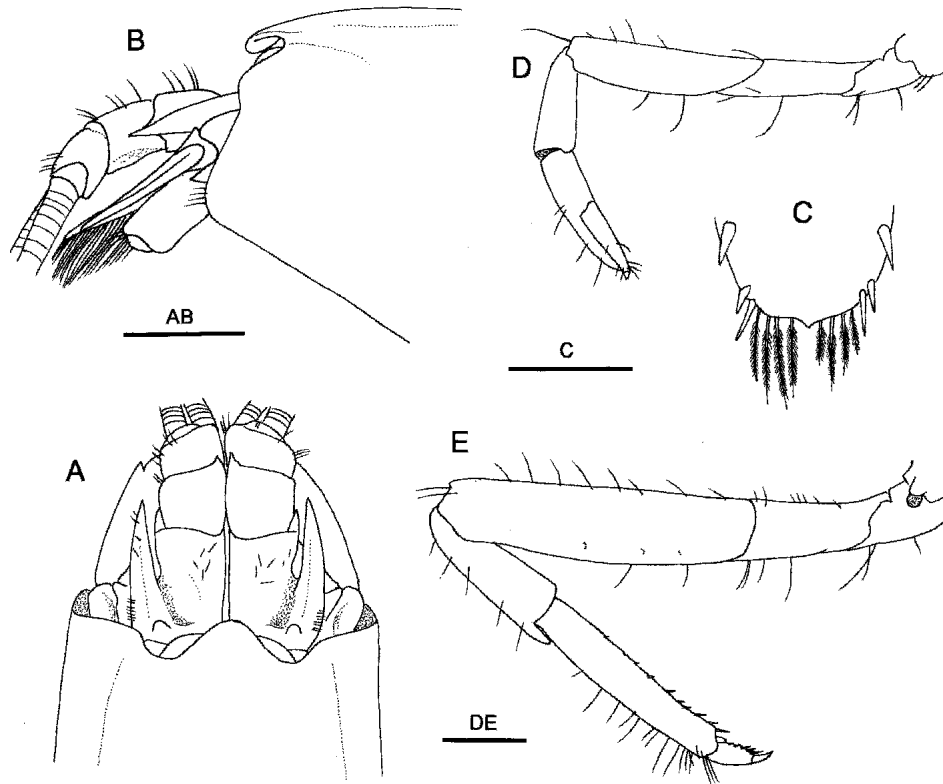


Figure 11. *Chorocaris chacei* (Williams & Rona, 1986). Juvenile (PCL 5.2 mm), Snake Pit, MNHN-Na. (A) Anterior part of carapace and cephalic appendages, dorsal view; (B) same, lateral view; (C) posterior part of telson, dorsal view; (D) left second pereopod, lateral view; (E) left third pereopod, lateral view.

Paratypes: Same data as holotype, one female (PCL 16.4 mm), USNM 228453.

#### Other Material

##### Lucky strike

DIVA 2 (DS *Nautile*): dive 09/920, June 11, 1994, slurp gun 10, one female (PCL 15.5 mm), MNHN-Na; dive 24/935, 1,600–1,700 m, June 30, 1994, box 1, six males (PCL 11.0–14.0 mm), 76 females (PCL 10.6–16.2 mm), MNHN-Na; same data, four females (PCL 14.9–17.7 mm); dive 24, site Eiffel Tower, 37°17.18'N, 32°16.29'W, 1,690 m, June 30, 1994, one female (PCL 21.5 mm), CBM-ZC 9391; same data, one ovigerous female (PCL 16.5 mm), MNHN-Na 16568; dive 25/936, 1,700 m, June 1, 1994, eight males (PCL 10.0–13.4 mm), nine females (PCL 11.6–13.2 mm), MNHN-Na. PICO (DS *Nautile*): dive 1271, 37°17.646'N, 32°16.888'W, 1,643 m, August 8, 1998; slurp gun 5, one female (PCL 14.8 mm), MNHN-Na 16569; same data, five females (PCL 10.1–16.1 mm); same data, three males (PCL 10.0–11.5 mm), six females (PCL 8.1–15.3 mm), two juveniles (PCL 6.1, 6.3 mm). ATOS (ROV *Victor*): dive 119–17, 37°17.33'N, 32°16.63'W, 1,689 m, July 17, 2001, slurp gun 7, 41 males (PCL 9.2–14.1 mm), 32 females (CL 11.5–ca 16.0 mm; larger specimens dissected for physiological study), MNHN-Na 16571; same data, two males (PCL 10.1, 15.3 mm), one female (PCL 9.0 mm), CBM-ZC 9392. EXOMAR (ROV *Victor* 6000): dive 269–20, 37°17.33'N, 32°16.52'W, 1,692 m, August 26, 2005, slurp gun 3, nine males (PCL 7.8–12.5 mm), 12 females (PCL 7.6–14.4 mm), three juveniles (PCL 4.8–6.0 mm), MNHN-Na 16572. MOMARETO (ROV *Victor*

6000): dive 294-11, site Eiffel Tower, 37°17.34'N, 32°16.53'W, 1,692 m, slurp gun 4, three females (PCL 11.1–11.2 mm), MNHN-Na 16573.

##### Rainbow

ATOS (ROV *Victor* 6000): dive 107-05, site Iris 13, 36°13.80'N, 33°54.20'W, 2,289 m, 30.06.2001, slurp gun 3, seven females (PCL 11.8–14.6 mm), MNHN-Na 16570.

##### TAG

EXOMAR (ROV *Victor* 6000): dive 260-11, 26°08.22'N, 44°49.56'W, 3626 m, August 13, 2005, slurp gun 3, one female (PCL 11.9 mm), 10 juveniles (PCL 5.5–7.4 mm), MNHN-Na 16574; same dive, slurp gun 5, four males (PCL 9.5–11.5 mm), 10 females (PCL 7.3–16.4 mm), CBM-ZC 9393; dive 262-13, 26°08.20'N, 44°49.55'W, 3,642 m, August 15, 2005, slurp gun 2, two males (PCL 6.3, 8.2 mm), four females (PCL 9.0–10.2 mm), one juvenile (PCL 5.6 mm), MNHN-Na 16575; same dive, slurp gun 4, four males (PCL 7.4–11.8 mm), two females (PCL 13.2, 17.0 mm), three juveniles (PCL 5.0–5.6 mm), MNHN-Na 16576.

##### Snake Pit

HYDROSNAKE (DS *Nautile*): HS 08, site Les Ruches, 23°22'N, 44°57'W, 3,478 m, 26 June 1988: 13 males (PCL 11.5–15.4 mm); same data, four males (PCL 12.6–17.4 mm; dissected for physiological study), MNHN-Na 11,871. DiversExpedition (DS *Alvin*): dive 3672, 23°22.10'N, 44°56.91'W, 3,492 m, July 14, 2001, six juveniles (PCL 4.8–6.1 mm), MNHN-Na.



*Logatchev*

DiversExpedition (DS *Alvin*): dive 3666, July 6, 2001, one female (PCL 13.5 mm), MNHN-Na 16577; dive 3668, 14°45.32'N, 44°58.79'W, 3,028 m, July 8, 2001, two males (PCL 6.8, 7.0 mm), two females (PCL 7.7, 8.6 mm), two juveniles (PCL 5.2, 6.7 mm), MNHN-Na 16578; no station data, 80 juveniles (CL 4.3–7.3 mm), MNHN-Na. SERPENTINE, dive 315–06, Irina 2, 14°45.18'N, 44°58.74'W, 3,021 m, March 18, 2007, slurp gun 5, one juvenile (CL 5.0 mm), MNHN-Na 16704; dive 316-07, same site, March 20, 2007, slurp gun 4, 46 juveniles (CL 4.3–6.8 mm), MNHN-Na 16705.

**Diagnosis**

Spawning females. Rostrum (Fig. 9A, C) somewhat reduced to broadly rounded lobe reaching or slightly overreaching anterior margins of eye-stalks or antennal lobes, directed downward; ventral surface slightly convex or flat. Carapace (Fig. 9A to D) with anterior part sloping anteriorly; no longitudinal depression on either side of midline; antennal lobe broadly rounded; pterygostomial expansion directed rather ventrally, exceeding beyond tip of antennal basicerite, rounded. Antennae (Fig. 9C, D) suboperculate, strongly directed downward, angle against horizontal line about 30–45°; distolateral tooth subacute or blunt, clearly separated from lamella by V-shaped notch. Scaphognathite of maxilla and caridean lobe of first maxilliped bearing numerous plumose seta-like structure on ventral surface; exopodal flagellum on first maxilliped completely reduced. First pereopod polymorphic (Fig. 10C, D). Uropodal protopod (Fig. 9E) with posterolateral projection subtriangular with subacute tip.

Non-spawning females and males. Rostrum (Fig. 10B) bluntly triangular, overreaching anterior margins of eye-stalks or tips of antennal lobes by less than half of its length; ventral surface slightly convex. Carapace (Fig. 10A, B) with broadly triangular or rounded antennal lobe, tip subacute or blunt; pterygostomial lobe directed forward, broadly rounded, less produced. Antennae (Fig. 10A, B) normal, only slightly directed downward. Lateral lobule of endopod of male first pleopod slightly produced (Fig. 10F). Appendix masculina (Fig. 10G) straight, 4 or 5 spiniform setae restricted to tip.

**Description**

See Williams and Rona (1986; as *Rimicaris*).

**Size**

Ovigerous female PCL 16.5 mm; males PCL 6.3–17.4 mm. The largest specimen is a female PCL 21.5 mm, TL ca. 76 mm.

**Variation**

We have found that the conformation of the anterior part of the carapace, including the rostrum, and antennae shows substantial ontogenetic change in adult *Chorocaris chacei*. The rostrum is reduced in size in the spawning females. The antennae are suboperculiform in spawning females, although they are normal in males and nonspawning females. The chela of the first cheliped can be robust in large specimens, but the variation does not show correlation to sex; large specimens do not always have robust chelae.

Komai and Segonzac (2006) showed a female specimen from Lucky Strike, of which the rostrum, antennal lobe, and

pterygostomial expansion terminate in an acute tooth. Among the specimens examined in this study, one male specimen from Lucky Strike also has acutely pointed rostrum and antennal lobe (Fig. 8F, G). We consider that these specimens represent an aberrant form of the species.

**Distribution**

Mid-Atlantic Ridge: Snake Pit (23°N), TAG (26°N), Lucky Strike (37°17'N), and Logatchev vent field, 1,600–3,650 m.

**Remarks**

As noted before, small paratypic specimens of *Chorocaris chacei* (five specimens of USNM 228454 and one specimen of MNHN-Na 10535) are the stage B juvenile of *Rimicaris exoculata*.

As mentioned earlier, three species of *Chorocaris* are very similar for one another. Characters useful for species discrimination are often affected by ontogenetic or individual variation. Spawning females of *C. chacei* can be rather easily distinguished from those of *C. vandoverae* and *C. paulexa* by the reduced rostrum, the lack of submedian longitudinal depressions on the dorsal surface of the carapace, and the broadly rounded antennal lobe of the carapace. In the latter two species, spawning females have submedian depressions on the dorsal surface of the carapace, more developed rostrum and clearly delineated antennal tooth. However, it is not easy to morphologically differentiate males and nonspawning females of the three species because of variation. Nevertheless, the distolateral tooth of the antennal scale appears more strongly reduced in *C. vandoverae* than in *C. chacei* and *C. paulexa*. In *C. vandoverae*, the distolateral tooth is blunt and strongly approximated to the distal lamella. In contrast, in *C. chacei* and *C. paulexa*, the distolateral tooth is subacute or blunt and is clearly separated from the lamella by a V-shaped notch. In general, males and nonspawning females of *C. chacei* differs from those of *C. vandoverae* and *C. paulexa* in the broadly rounded pterygostomial projection. In the latter two species, the pterygostomial projection tapers distally. With regard to males, *C. chacei* can be distinguished from *C. vandoverae* by the armature of the appendix masculina. In *C. chacei*, the appendix masculina is armed with four or five terminal or subterminal spines, whereas in *C. vandoverae*, it bears numerous spines including one or two rows extending onto the dorsal surface. No information on male morphology is available for *C. paulexa*. Furthermore, the available material suggests that *C. chacei* attains maturity at size fairly larger than *C. vandoverae* and *C. paulexa*. Ovigerous specimen(s) are PCL 16.5 mm in *C. chacei*, PCL 6.9–11.7 mm in *C. vandoverae*, and PCL 9.6 mm in *C. paulexa*. In addition, the largest female is PCL 17.4 mm in *C. chacei*, PCL 13.4 mm in *C. vandoverae* and PCL 9.6 mm in *C. paulexa*.

Martin and Hessler (1990) cited the size of the carpal grooming apparatus of the first pereopod (as cleaning brush) and the shape of the antennular stylocerite in discriminating *C. vandoverae* from *C. chacei*. However, these two characters are difficult to use because of the intraspecific variability in both species.

***Chorocaris vandoverae* Martin and Hessler 1990 (Fig. 12)**

*Chorocaris vandoverae* Martin and Hessler 1990: 2, Figures 1, 2, 3 a to e; Shank 1997:194; Shank et al. 1999: 246 (Table 1),

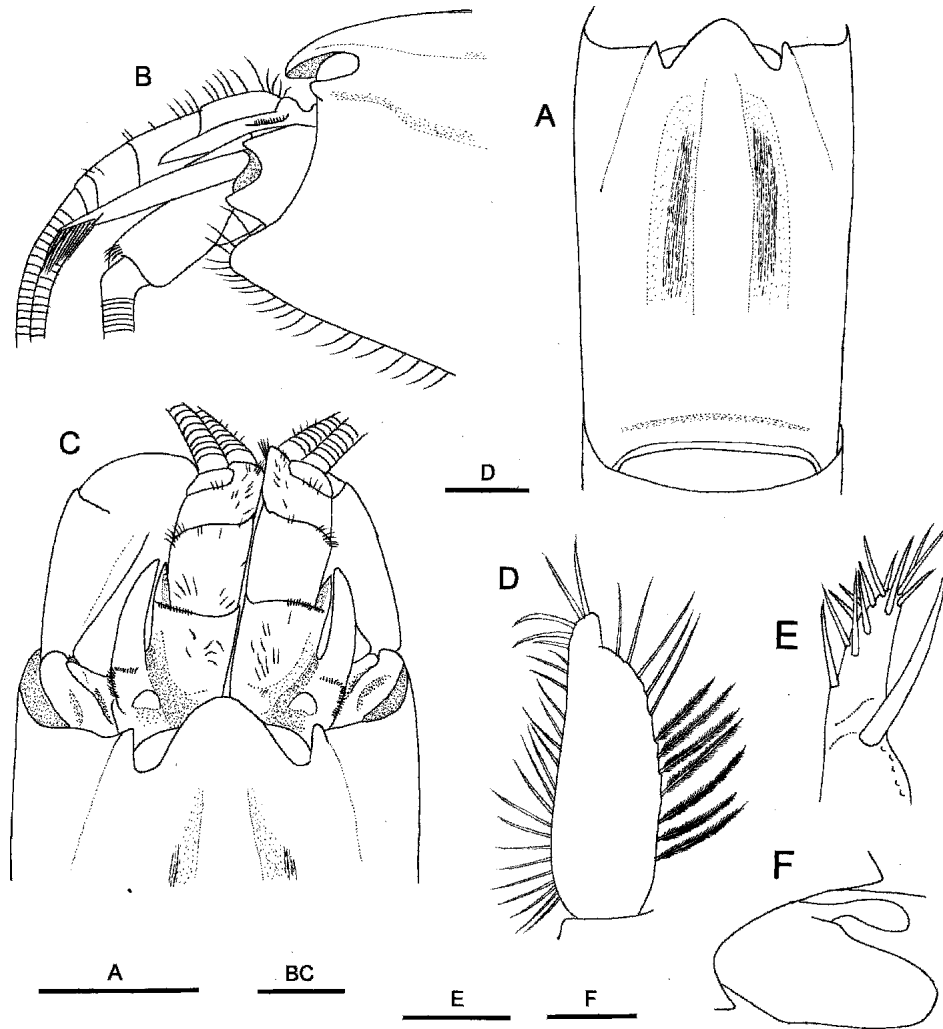


Figure 12. *Chorocaris vandoverae* Martin & Hessler, 1990. (A–C, F) Ovigerous female (PCL 12.0 mm), JAMSTEC 004961–004982, Alice Springs Field, Mariana Back Arc Basin; (D, E) male (cl mm), same lot. (A) Carapace, dorsal view; (B) anterior part of carapace and cephalic appendages, lateral view; (C) same, dorsal view; (D) endopod of left first pleopod, ventral view; (E) appendices interna and masculina of left second pleopod, mesial view; (F) protopod of left uropod, dorsolateral view. Scale bars: 5 mm for A; 2 mm for B, C; 1 mm for F; 0.5 mm for E.

247 (Table 2); Martin and Shank 2005: 184; Martin and Haney 2005: 465; Komai and Segonzac 2006: 423, Figures 1–4.

#### Type Material

Holotype. Mariana Back Arc Basin. DSV *Alvin*, dive 1843, Alice Spring vent field, 18°12.599' N, 144°42.231' E, 3,640 m, May 4, 1987, female (PCL 13.4 mm), USNM 243946.

Paratypes: Same data as holotype, 10 females (PCL 8.0–12.6 mm), USNM 243947.

#### Other Material

Mariana Back Arc Basin. DSV *Shinkai 6500*, dive 355, Alice Springs vent field, 18°12.8' N, 144°42.4' E, 3,600 m, July 7, 1996, two males (PCL 5.8, 8.0 mm), four nonovigerous females (PCL 4.9–7.9 mm), six ovigerous females (PCL 6.9–11.7 mm), JAMSTEC 004961–004972.

#### Diagnosis

Rostrum (Fig. 12A to C) large, bluntly triangular or rounded, overreaching eye-stalks or antennal tooth by 0.2–0.5 of its length; ventral surface notably convex. Carapace (Fig. 12A to C) with anterior part not strongly sloping anteriorly even in spawning females; shallow longitudinal depressions, ornamented with irregular pattern of longitudinal striae, present on dorsal surface either side of midline in ovigerous females; antennal tooth showing as small, blunt prominence; pterygostomial projection directed forward, somewhat tapering distally, reaching tip of ventrolateral tooth of basicerite, terminating in rounded tip. Antennae (Fig. 12B, C) not strongly operculiform, slightly directed downward, angle against horizontal plane of carapace 10–15°; distolateral tooth blunt, closely approximated to lamella, thus apparently inconspicuous. Scaphognathite of maxilla and caridean lobe of first maxilliped lacking plumose seta-like structure on ventral surfaces; exopodal flagellum of first maxilliped showing as small triangular process practically obscured by dense setae. First

pereopod apparently nonpolymorphic. Distolateral lobe of endopod of first pleopod not delineated (Fig. 12D). Appendix masculina (Fig. 12E) slightly curved, with more than 10 spiniform setae extending beyond midlength on dorsomesial margin. Uropodal protopod with posterolateral projection suboval (Fig. 12F).

#### Description

See Martin and Hessler (1990).

#### Size

Ovigerous females PCL 6.9–11.7 mm; males PCL 5.8–8.0 mm. The largest specimen is a female PCL 13.4 mm, TL ca. 48 mm.

#### Variation

Spawning females have shallow submedian depressions on the dorsal surface of the carapace, which are not present in males and nonspawning females.

#### Distribution

So far known only from Alice Springs and Burke vent fields, Mariana Back-Arc Basin, western Pacific, 3,640–3,660 m.

#### Remarks

*Chorocaris vandoverae* appears closest to *C. paulexa*. Differences between the two species are discussed under the account of the latter species.

#### *Chorocaris paulexa* Martin and Shank 2005 (Fig. 13)

*Chorocaris paulexa* Martin and Shank 2005: 186, Figures 1–8; Martin and Haney 2005: 464; Komai and Segonzac 2006: 422, Figures 1–3.

#### Type material

Holotype: Southern East Pacific Rise. DSV *Alvin*: dive 3296, Rapa Nui Homer vent site, 17°37.220'S, 113°15.123'W, 2,596 m, October 27, 1998, Hoover slurp, ovigerous female (PCL 7.5 mm), LACM CR 1998-151.1.

Paratype: Same data as holotype, one female (PCL 9.6 mm), LACM CR 1998.151.2.

#### Diagnosis

Rostrum (Fig. 13A, B) bluntly triangular, overreaching eye-stalks or antennal lobes by half of its length; ventral surface convex. Carapace (Fig. 13A, B) with anterior part slightly sloping anteriorly; shallow longitudinal depressions, ornamented with irregular pattern of minute longitudinal striae, present on dorsal surface either side of midline in ovigerous female; antennal tooth showing as blunt prominence; pterygostomial expansion not reaching tip of ventrolateral tooth of antennal basicerite, triangular, terminating in subacute tip. Antennae (Fig. 13B) not operculiform, slightly directed downward, angle against horizontal plane of carapace less than 10°; distolateral tooth subacute, distinctly separated from lamella by V-shaped notch. Scaphognathite of maxilla and caridean lobe of first maxilliped lacking plumose seta-like structure on ventral surfaces; exopodal flagellum of first maxilliped showing as small triangular process. First pereopod apparently nonpolymorphic. Male unknown. Uropodal protopod with posterolateral projection triangular with subacute tip (Fig. 13C).

#### Description

See Martin and Shank (2005).

Size: Ovigerous female PCL 7.5 mm, males unknown.

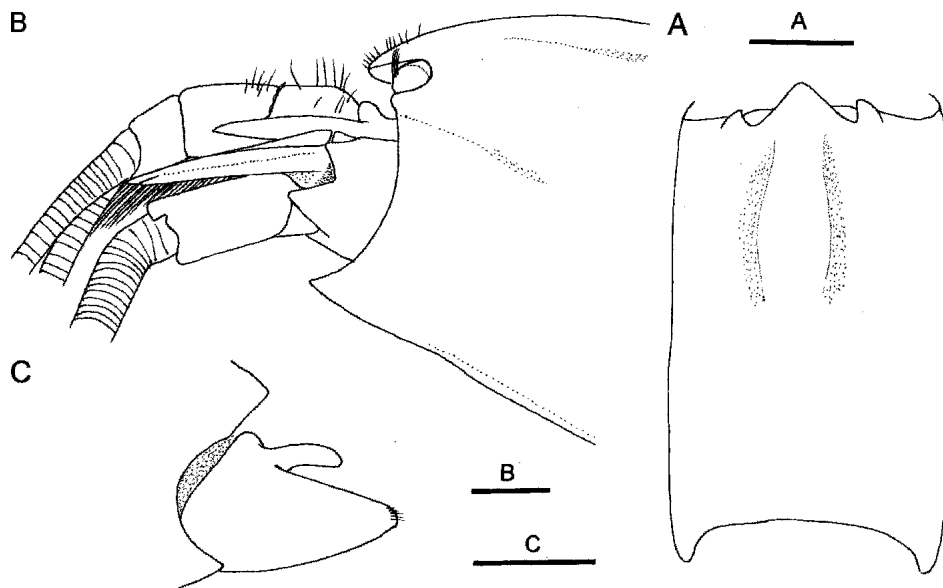


Figure 13. *Chorocaris paulexa* Martin & Shank, 2005. Holotype, ovigerous female (PCL 7.7 mm), LACM CR 1998–151.1, Homer Vent, southern East Pacific Rise. (A) Carapace, dorsal view; (B) anterior part of carapace and cephalic appendages, lateral view; (C) protopod of left uropod, dorsolateral view. Scale bars: 2 mm for A; 1 mm for B, C.

### Variation

The single ovigerous female has shallow submedian depressions on the dorsal surface of the carapace, whereas the non-ovigerous female lack such depressions.

### Distribution

So far known only from hydrothermal vent sites on the southern East Pacific Rise (17°–21°S), 2,573–2,832 m (Martin & Shank 2005).

### Remarks

*Chorocaris paulexa* differs from *C. vandoverae* in the subacutely pointed pterygostomial projection of the carapace and subacutely pointed posterolateral projection of the uropodal protopod. In *C. vandoverae*, the pterygostomial projection is distally rounded; and the posterolateral projection of the uropodal protopod is bluntly pointed usually. The rostrum is comparatively smaller in *C. paulexa* than in *C. vandoverae* (Fig. 13A and 12A). The distolateral tooth of the antennal scale is clearly separated from the lamella in *C. paulexa*, rather than closely approximated to the lamella in *C. vandoverae*.

### BIOGEOGRAPHY

Five species treated in this study constitute a monophyletic assemblage within Alvinocarididae. The general geographical range of this assemblage is widespread in the world oceans, although the range of each species is restricted to a particular area. *Rimicaris exoculata* and *Chorocaris chacei* have a wide longitudinal distribution along the Mid-Atlantic Ridge, and the former has been recorded from 37°N to 4°S, and the latter from 37°N to 14°N. The other three species are restricted to narrow areas. *Rimicaris kairei* is known only from two vent fields (Kairei & Edmond) at the Rodriguez Triple Junction of the Central Indian Ridge, Indian Ocean. *Chorocaris vandoverae* is

known from Burke and Alice Springs fields on the Mariana Back Arc Basin, northwestern Pacific Ocean. *Chorocaris paulexa* is so far limited to the Easter Microplate area on the southern East Pacific Rise. The two *Rimicaris* species are distributed in the Atlantic and Indian Oceans respectively, and the possible sister species of the *Rimicaris* clade, *C. chacei*, occurs in the Atlantic Ocean. Other two species of *Chorocaris*, *C. vandoverae*, and *C. paulexa*, occur in the western and eastern Pacific, respectively. It is remarkable that species referable to *Chorocaris* has not been collected from the Indian Ocean, whereas species referable to *Rimicaris* has not been found in the Pacific Ocean in spite of recent active surveys. Such distributional pattern would seem to suggest that these taxa are relicts, but Shank et al. (1999) argued that vent shrimps comprise the youngest vent- and seep-associated diversification observed to date.

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