A new species of *Rimicaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vent fields on the Mid-Cayman Spreading Centre, Caribbean

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Rimicaris hybisae sp. nov. is described from hydrothermal vent fields on the world’s deepest seafloor spreading centre, the Mid-Cayman Spreading Centre (MCSC), Caribbean, at depths of 2300–4960 m. The new species is described and illustrated on the basis of 17 specimens. Brief notes on the distribution and habitat of the new species are provided. Molecular phylogenetic data from mitochondrial COI (460 base pair (bp)), 16S ribosomal RNA (549 bp) and nuclear 18S ribosomal RNA (576 bp) regions is used to complement the description. Morphological variation within *R.* hybisae sp. nov. and morphological affinities with previously described species are discussed. Based on morphological and molecular evidence, the new species is provisionally assigned to the genus *Rimicaris*, and differs from all known species in the genus by a distinctive pair of ‘pores’ on the posterior lobes of its four-lobed dorsal organ. An emended diagnosis for *Rimicaris* is provided. Rimicaris hybisae sp. nov. is the first taxon to be described from MCSC vent fields. This record extends the known geographical range of *Rimicaris* into the Caribbean Sea and constitutes the deepest documented occurrence of alvinocaridid shrimp.

**Keywords:** Crustacea, Decapoda, Caridea, Alvinocarididae, *Rimicaris*, new species, Cayman, hydrothermal vents

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**INTRODUCTION**

All known species of the caridean family Alvinocarididae Christoffersen, 1986 occur exclusively in hydrothermal vents or cold (brine and hydrocarbon) seeps (see Table 1 and references therein). Alvinocarids are known from a considerable number of vents and seeps in the Atlantic, Pacific and Indian Oceans (Table 1). Alvinocaridid shrimp are the dominant macrofaunal invertebrates at several vents along the Mid-Atlantic Ridge (MAR) (e.g. Van Dover et al., 1988; Segonzac, 1992; Gebrik et al., 1993, 1997; Van Dover, 2000; Martin & Shank, 2005) and at known vent fields in the Indian Ocean (Hashimoto et al., 2001; Van Dover et al., 2001; Watabe & Hashimoto, 2002). The Alvinocarididae presently comprises 26 described species in 8 genera, all from chemosynthetic environments in the bathymetric range 252–4088 m (Table 1).

*Alvinocaris* Williams & Chace, 1982 is presently the only genus known to inhabit both hydrothermal vents and cold seeps (Table 1). *Alvinocaris, Rimicaris* Williams & Rona, 1986, *Chorocaris* Martin & Hessler, 1990 and *Opaephe* Williams & Dobbs, 1995 were originally assigned to the caridean family Bresiliidae Calman, 1896 (see Martin & Davis, 2001; Komai & Segonzac, 2003), whereas the family Mirocarididae Vereshchaka, 1997 was established to accommodate the genus *Mirocaris* Vereshchaka, 1997. Komai & Segonzac (2003) subsequently assigned all these genera to the Alvinocarididae, and synonymized the family Mirocarididae with the Alvinocarididae.

The family Bresiliidae is now only represented by two genera (De Grave et al., 2009), *Bresilia* Calman, 1896 and the monotypic *Encomienda* Wicksten, 1989, neither of which are known to occur in chemosynthetic habitats (Wicksten, 1989; Komai & Yamada, 2010, 2011). The family Alvinocarididae (Christoffersen, 1986, 1990; Segonzac et al., 1993; Komai & Segonzac, 2003) is now regarded as a valid monophyletic family (e.g. Komai & Segonzac, 2005, 2008; Martin & Haney, 2005; De Grave et al., 2009), morphologically distinct from opportunistic shrimp species recorded from vents and seeps (see Martin & Haney, 2005; Desbruyères et al., 2006 for recent reviews).

Recently, two high-temperature hydrothermal vent fields and chemosynthetic communities were discovered on the world’s deepest seafloor spreading centre, the Mid-Cayman Spreading Centre (MCSC), Caribbean (Connelly et al., in press). The ~110 km long, ultralow-spreading (15 mm yr⁻¹) MCSC has been active for approximately 49 My (Rosencrantz et al., 1988; German et al., 2010) and is located in a deep trough, geographically and tectonically isolated from the global mid-ocean ridge system (Ballard et al., 1979).

The Beebe Vent Field (BVF) consists of a sulphide mound (80 m diameter, 50 m height) surmounted with several actively
venturing sulphide chimneys and, at 4960 m, it is the world’s
deepest known vent field (Connelly et al., in press). The Von
Damm Vent Field (VDVF) occurs 30 km from the BVF, on the
upper slopes of an off-axis massif, at 2300 m depth (Connelly et al., in press). The VDFV comprises a sulphide mound (100 m diameter, 30 m height) venting predominantly
clear, buoyant, high-temperature (>140 °C) fluids from orifices
at its peak (Connelly et al., in press). Study of the fauna
inhabiting these unique vents has the potential to enhance
current understanding of the dispersal, isolation, and evolution
of vent taxa and patterns of vent biogeography.

The fauna at both vent fields is dominated by dense aggre-
gations of *Rimicaris hybisae* (Figure 1), a new species of alvinocaridid shrimp, with a greatly reduced rostrum, and a
four-lobed dorsal organ, similar to the photoreceptor of
*Rimicaris* (Van Dover et al., 1989). *Rimicaris hybisae* sp.

**Table 1.** Summary of known geographical distribution, bathymetric range and habitat of alvinocaridid shrimp species (confirmed locations and fully
described species only).

<table>
<thead>
<tr>
<th>Species</th>
<th>Site(s)</th>
<th>Depth (m)</th>
<th>Habitat</th>
<th>Primary references</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alvinocaridinidae formosa</em></td>
<td>North-east Taiwan: Gueishandoa</td>
<td>252–275</td>
<td>Vent</td>
<td>Komai &amp; Chan, 2010</td>
</tr>
<tr>
<td><em>Alvinocaris brevitelsonis</em></td>
<td>OT: Minami–Ensei Knoll</td>
<td>705</td>
<td>Vent</td>
<td>Kikuchi &amp; Hashimoto, 2000 (see also Komai &amp; Segonzac, 2005)</td>
</tr>
<tr>
<td><em>Alvinocaris chelys</em></td>
<td>North-east Taiwan: Gueishandoa</td>
<td>252–300</td>
<td>Vent</td>
<td>Komai &amp; Chan, 2010</td>
</tr>
<tr>
<td><em>Alvinocaris dissimilis</em></td>
<td>OT: Minami–Ensei Knoll</td>
<td>705</td>
<td>Vent</td>
<td>Komai &amp; Segonzac, 2005</td>
</tr>
<tr>
<td><em>Alvinocaris komai</em></td>
<td>ELSC: ABE, Kilo Moana, TowCam, Tu' i Malila</td>
<td>1880–2700</td>
<td>Vent</td>
<td>Zelnio &amp; Hourdez, 2009</td>
</tr>
<tr>
<td><em>Alvinocaris longirostris</em></td>
<td>OT: Iheya Ridge, Hatoma Knoll; SB: Off Hatsushima site</td>
<td>1053–1627</td>
<td>Vent and seep</td>
<td>Kikuchi &amp; Ohta, 1995; Fujikura et al., 1995; Watabe &amp; Miyake, 2000; Ohta &amp; Kim, 2001</td>
</tr>
<tr>
<td><em>Alvinocaris lasca</em></td>
<td>GR: Rose Garden; EPR: 9°N</td>
<td>2450–3250</td>
<td>Vent</td>
<td>Williams &amp; Chace, 1982; Shank et al., 1999</td>
</tr>
<tr>
<td><em>Alvinocaris markensis</em></td>
<td>MAR: Lucky Strike; Rainbow; Broken Spur; TAG; Snake Pit; Logatchev</td>
<td>1693–3650</td>
<td>Vent</td>
<td>Williams, 1988; Shank et al., 1999</td>
</tr>
<tr>
<td><em>Alvinocaris methanophila</em></td>
<td>Blake Ridge Diapir</td>
<td>2155</td>
<td>Seep</td>
<td>Komai et al., 2005</td>
</tr>
<tr>
<td><em>Alvinocaris muricola</em></td>
<td>GoM: Florida Escarpment; Barbados Accretionary prism; West African equatorial margin, Congo Basin; Blake Ridge Diapir</td>
<td>1697–3277</td>
<td>Seep</td>
<td>Williams, 1988; Komai &amp; Segonzac, 2005; Komai et al., 2005</td>
</tr>
<tr>
<td><em>Alvinocaris niwa</em></td>
<td>KR: Rumble V Seamount, Brothers Caldera</td>
<td>360–1538</td>
<td>Vent</td>
<td>Webber, 2004</td>
</tr>
<tr>
<td><em>Alvinocaris stactophila</em></td>
<td>GoM: Louisiana Slope</td>
<td>534</td>
<td>Seep</td>
<td>Williams, 1988</td>
</tr>
<tr>
<td><em>Alvinocaris williamsi</em></td>
<td>MAR: Menez Gwen</td>
<td>850–865</td>
<td>Vent</td>
<td>Shank &amp; Martin, 2003</td>
</tr>
<tr>
<td><em>Chorocaris chacei</em></td>
<td>MAR: Menez Gwen</td>
<td>1600–3650</td>
<td>Vent</td>
<td>Williams &amp; Rona, 1986; Komai &amp; Segonzac, 2008; Copley et al., in press</td>
</tr>
<tr>
<td><em>Chorocaris palaea</em></td>
<td>EPR: 17°–21°S</td>
<td>2573–2832</td>
<td>Vent</td>
<td>Martin &amp; Shank, 2005</td>
</tr>
<tr>
<td><em>Chorocaris vandoverae</em></td>
<td>MBAR: Alice Springs, Burke</td>
<td>3640–1660</td>
<td>Vent</td>
<td>Martin &amp; Hessler, 1990</td>
</tr>
<tr>
<td><em>Mirotocaris fortunata</em></td>
<td>MAR: Menez Gwen; Lucky Strike; TAG; Snake Pit; Logatchev; Ashadze; Turtle Pits</td>
<td>850–3480</td>
<td>Vent</td>
<td>Martin &amp; Christiansen, 1995; Vereshchaka, 1997; Shank et al., 1999; Komai &amp; Segonzac, 2003; Komai et al., 2007; Fabri et al., 2011; Copley et al., 2011</td>
</tr>
<tr>
<td><em>Mirotocaris indica</em></td>
<td>CIR: Kairei, Edmond</td>
<td>2422–3300</td>
<td>Vent</td>
<td>Komai et al., 2006</td>
</tr>
<tr>
<td><em>Opepele loihi</em></td>
<td>Hawaii: Loihi Seamount</td>
<td>980</td>
<td>Vent</td>
<td>Williams &amp; Dotts, 1995</td>
</tr>
<tr>
<td><em>Opepele susannae</em></td>
<td>MAR: Sisters Peak; Lilliput; Semenov</td>
<td>1500–2986</td>
<td>Vent</td>
<td>Komai et al., 2007; Beltenev et al., 2009</td>
</tr>
<tr>
<td><em>Opepele vavili</em></td>
<td>MAR: Broken Spur</td>
<td>3900</td>
<td>Vent</td>
<td>Lavinia &amp; Vereshchaka, 2010</td>
</tr>
<tr>
<td><em>Rimicaris exoculata</em></td>
<td>MAR: Møytirra; Rainbow; Lucky Strike; Broken Spur; TAG; Snake Pit; Logatchev; Ashadze; Mephisto</td>
<td>1700–4088</td>
<td>Vent</td>
<td>Williams &amp; Rona, 1986; Komai et al., 2007; Komai &amp; Segonzac, 2008; Copley et al., in press</td>
</tr>
<tr>
<td><em>Rimicaris kairei</em></td>
<td>CIR: Kairei; Edmond</td>
<td>2415–3320</td>
<td>Vent</td>
<td>Watabe &amp; Hashimoto, 2002</td>
</tr>
<tr>
<td><em>Rimicaris hybisae</em> sp. nov.</td>
<td>MCSC: Beebe; Von Damm</td>
<td>2300–4960</td>
<td>Vent</td>
<td>This study</td>
</tr>
<tr>
<td><em>Shinkaicaris leurokolas</em></td>
<td>OT: Minami–Ensei Knoll</td>
<td>700</td>
<td>Vent</td>
<td>Kikuchi &amp; Hashimoto, 2000; Komai &amp; Segonzac, 2005</td>
</tr>
</tbody>
</table>

CIR, Central Indian Ridge; ELSC, East Lau Spreading Centre; EPR, East Pacific Rise; GoM, Gulf of Mexico; GR, Galapagos Rift; KR, Kermadec Ridge, New Zealand; LB, Lau Basin; MAR, Mid-Atlantic Ridge; MBAR, Mariana Back-Arc Basin; MCSC, Mid-Cayman Spreading Centre; OT, Okinawa Trough; SB, Sagami Bay.
A NEW SPECIES OF RIMICARIS FROM MCSC VENTS

nov., described and illustrated herein, is the first taxon to be described from vent fields on the MCSC. In addition to enhancing existing knowledge about biodiversity, this record extends the known geographical range of *Rimicaris* (previously only recorded from Atlantic and Indian Ocean vents; Table 1) westwards into the Caribbean Sea, and extends the known bathymetric range of the Alvinocarididae by 872 m.

**MATERIALS AND METHODS**

The specimens were collected during the 44th cruise of the RRS ‘James Cook’ in April 2010 from Beebe (4960 m) and Von Damm (2300 m) hydrothermal vent fields on the MCSC, Caribbean. Shrimp samples were taken using a grab (Von Damm) and suction sampler (Beebe) attached to the maneuverable TV grab HyBIS (Hydraulic Benthic Interactive Sampler), together with still photographs and video recordings of them in situ at both sites. Material for morphological study was immediately fixed in 10% neutralized formalin and subsequently transferred to 80% industrial methylated spirits on return to the laboratory. Material for molecular analysis was immediately placed in 100% ethanol.

The measurements taken for each specimen (Table 2) were measured to the nearest 0.1 mm using Vernier callipers. Post-orbital carapace length (CL) was measured from the mid-point of the posterodorsal margin to the level of the posterior margin of the orbit. Maximum total length (TL) was measured from the posterior margin of the telson to the anterior margin of the antennal scale. Maximum carapace width (CW) and maximum carapace depth (CD) were measured at the widest and deepest points of the carapace respectively. Specimen size herein is indicated by post-orbital CL.

Individuals were sexed under a dissecting microscope. Males were distinguished by an asymmetrical mesial extension on the endopod of pleopod 1 and the presence of the appendix masculina on the second pleopod (Williams, 1988). The sex of specimens CL 6.7 mm and smaller could not be determined by this method; those specimens are referred to as juveniles.

Fig. 1. *Rimicaris hybisae* sp. nov., live specimen, from the Beebe Vent Field, Mid-Cayman Spreading Centre. P denotes twin pores in the dorsal organ. 69 × 57 mm (150 × 150 DPI).

**Table 2.** Morphological variation in *Rimicaris hybisae* sp. nov. Mid-Cayman Spreading Centre vent fields are abbreviated as VDVF (Von Damm) and BVF (Beebe).

<table>
<thead>
<tr>
<th>Site</th>
<th>Cat. no.</th>
<th>Sex</th>
<th>Type status</th>
<th>CL (mm)</th>
<th>CW (mm)</th>
<th>CD (mm)</th>
<th>CW/CD</th>
<th>TL (mm)</th>
<th>Teeth AS4 left</th>
<th>Teeth AS4 right</th>
<th>Teeth AS5 left</th>
<th>Teeth AS5 right</th>
</tr>
</thead>
<tbody>
<tr>
<td>VDVF</td>
<td>NHMUK 2011.8054</td>
<td>Female</td>
<td>Holotype</td>
<td>15.3</td>
<td>12.6</td>
<td>7.5</td>
<td>1.7</td>
<td>46.6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>VDVF</td>
<td>NHMUK 2011.8055</td>
<td>Male</td>
<td>Paratype</td>
<td>9.4</td>
<td>8.8</td>
<td>5.2</td>
<td>1.7</td>
<td>32.5</td>
<td>0</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>BVF</td>
<td>NHMUK 2011.8056</td>
<td>Female</td>
<td>Paratype</td>
<td>10.8</td>
<td>9.3</td>
<td>5.4</td>
<td>1.7</td>
<td>39.7</td>
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<td>0</td>
</tr>
<tr>
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<td>NHMUK 2011.8057</td>
<td>Male</td>
<td>Paratype</td>
<td>10.6</td>
<td>8.3</td>
<td>7.1</td>
<td>1.2</td>
<td>35.1</td>
<td>1</td>
<td>0</td>
<td>4</td>
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<td>NHMUK 2011.8058</td>
<td>Male</td>
<td>Paratype</td>
<td>10.0</td>
<td>7.4</td>
<td>6.4</td>
<td>1.2</td>
<td>36.6</td>
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<td>BVF</td>
<td>NHMUK 2011.8059</td>
<td>Male</td>
<td>Paratype</td>
<td>10.8</td>
<td>8.7</td>
<td>6.9</td>
<td>1.3</td>
<td>37.7</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
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<td>BVF</td>
<td>NHMUK 2011.8060</td>
<td>Male</td>
<td>Paratype</td>
<td>10.0</td>
<td>8.1</td>
<td>5.8</td>
<td>1.4</td>
<td>33.7</td>
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<td>BVF</td>
<td>NHMUK 2011.8061</td>
<td>Male</td>
<td>Paratype</td>
<td>11.8</td>
<td>9.9</td>
<td>7.2</td>
<td>1.4</td>
<td>36.2</td>
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<tr>
<td>BVF</td>
<td>NHMUK 2011.8062</td>
<td>Female</td>
<td>Paratype</td>
<td>7.0</td>
<td>x</td>
<td>x</td>
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<td>NHMUK 2011.8063</td>
<td>Male</td>
<td>Paratype</td>
<td>10.9</td>
<td>x</td>
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<td>Paratype</td>
<td>9.0</td>
<td>7.9</td>
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<td>NHMUK 2011.8065</td>
<td>Juvenile</td>
<td>Paratype</td>
<td>6.7</td>
<td>4.9</td>
<td>4.1</td>
<td>1.2</td>
<td>22.6</td>
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<td>NHMUK 2011.8066</td>
<td>Juvenile</td>
<td>Paratype</td>
<td>5.1</td>
<td>3.5</td>
<td>2.9</td>
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<td>Paratype</td>
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<td>Paratype</td>
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<td>x</td>
<td>x</td>
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<td>Paratype</td>
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<td>3.3</td>
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<td>NHMUK 2011.8070</td>
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<td>Paratype</td>
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<td>2.8</td>
<td>1.9</td>
<td>1.5</td>
<td>13.7</td>
<td>0</td>
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</tr>
</tbody>
</table>

CL, post-orbital carapace length; CW, maximum carapace width; CD, maximum carapace depth; TL, total length; AS4, abdominal somite 4, posterolateral margin; AS5, abdominal somite 5, posterolateral margin; ovi, ovigerous; x, measurement could not be taken due to condition of carapace; *, with visibly mature ovary.
Abdominal muscle for DNA extraction was cut from the shrimp of ethanol-preserved specimens (from both the Beebe and Von Damm vent fields) and the carapace removed. Genomic DNA was extracted using the CTAB (cetyltrimethyl ammonium bromide) procedure (Doyle & Dickson, 1987). Regions of the mitochondrial genes cytochrome c oxidase subunit I gene (COI) and 16S ribosomal RNA, and of the nuclear 18S ribosomal RNA gene were amplified by performing polymerase chain reactions (PCR).

The COI region was amplified with universal primers LCO1490 and HCO2198 (Folmer et al., 1994). The 20 µl amplification mixture contained 1X buffer reagent (200 mM Tris pH 8.8, 500 mM KCL, 0.1% Tritxon X-100, 2 mg/ml bovine serum albumen), 2 mM MgCl₂, 0.2 mM of each dNTP, 0.5 mM of each primer, 1 U Taq DNA polymerase (Bioline), 5 µl of template DNA and sterile H₂O to final volume. Thermal cycling conditions were: 94°C/2 minutes; followed by 30 cycles at (94°C/35 seconds; 45°C/35 seconds; 72°C/1:20 minutes) and 35 cycles at (94°C/35 seconds; 50°C/35 seconds; 72°C/1:20 minutes) with a final extension of 72°C/10 minutes.

For the 16S gene, PCR amplifications were performed using the universal primers 16Sar and 16Sbr (Palumbi, 1996) and a 20 µl amplification mixture: 1X reaction buffer (same as for COI), 2.5 mM MgCl₂, 0.13 mM of each dNTP, 0.38 mM of each primer, 1 U Taq DNA polymerase (Bioline), 2.5 µl of template DNA and sterile H₂O to final volume. Thermal cycling conditions were: 94°C/1 minutes; 30 cycles at (94°C/30 seconds; 52°C/1 minutes; 72°C/2 minutes) and 72°C/5 minutes.

Polymerase chain reaction amplifications of the 18S gene were performed using universal primers 18SuniF and 18SuniR (Sogin, 1990) in an amplification mixture as described for COI. Thermal cycling conditions were: 95°C/5 minutes; 30 cycles at (94°C/1 minute; 64°C/1 minute; 72°C/2:30 minutes) and 72°C/10 minutes. Negative controls were included as standard and sterile procedures were consistently followed for all PCR experiments.

Polymerase chain reaction products were purified with the ExoAP treatment by adding the following ExoAP mixture to 15 µl PCR product: 0.2 µl 10X ExoAP buffer (50 mM Bis-Tris, 1mM MgCl₂, 0.1 mM ZnSO₄), 0.05 µl 5000 U/ml Antarctic Phosphatase (New England Biolabs: Ipswich, MA), 0.05 µl 20000 U/ml Exonuclease I, and 3.7 µl sterile H₂O and thermal-cycler incubation (37°C/60 minutes; 85°C/15 minutes). Sequencing reactions were performed using BigDye Terminator Reactions following the manufacturer’s protocol (Applied Biosystems: Foster, CA) with the same primer sets used for amplifications. For COI, the thermal-cycler reaction was performed as: 94°C/30 seconds followed by 25 cycles at (94°C/15 seconds; 50°C/15 seconds; 60°C/3 minutes). For 16S and 18S the PCR reaction products were purified with the AMPure magnetic bead system (Agencourt: Morrisville, NC) following the manufacturer’s protocol and were subsequently run on an ABI 3730x1 DNA Analyzer (Applied Biosystems International).

The sequence strands for each gene were proof-read and assembled with CodonCode Aligner, version 3.7-1 (CodonCode Corporation, Dedham, MA, USA), to produce a continuous fragment. Sequences were compared with those in GenBank using the nucleotide BLAST program (NCBI Basic Alignment Search Tool) and manually aligned in BioEdit (Hall, 1999). Phylogenetic trees were constructed with MEGAs (Tamura et al., 2011) using the neighbour-joining (NJ) (Saitou & Nei, 1987) and maximum-likelihood (ML) (Kimura, 1980) methods on 460- and 540-base pair (bp) alignments for COI and 18S respectively. Bootstrap values were calculated on 1000 re-sampling replicates.

GenBank accession numbers for partial sequences of the 16S, COI and 18S regions are JN850606, JN850607 and JN850608 respectively.

SYSTEMATICS
Order DECAPODA Latreille, 1802
Infraorder CARIDEA Dana, 1852
Superfamily BRESILOIDEA Calman, 1896
Family ALVINOCARIDIDAE Christoffersen, 1986
Genus Rimicaris Williams & Rona, 1986

TYPE SPECIES
Rimicaris exoculata Williams & Rona, 1986

DIAGNOSIS (EMENDED)
Carapace greatly inflated laterally, distinctly broader than pleon, dorsal surface rounded, pitted with scattered, shallow punctuations. Ptyerygostomial expansion produced, exceeding antennal lobe, covering greater part of antennal basicerite, rounded or blunt. Rostrum reduced to broadly rounded lobe. Eyes lacking pigment, eyestalks flattened, greatly reduced and medi- ally fused. Antenna scale broadly oval, bearing distolateral transverse suture. Mandible with two-segmented palp, distinct separation between incisor and molar processes. Maxilla with scaphognathite greatly expanded anteriorly and conspicuously setose on dorsal and ventral surfaces. First maxilliped with greatly expanded exopod, similar to scaphognathite, conspicuously setose on dorsal and ventral surfaces. Third maxilliped with three long segments and coxa.

COMPOSITION
Rimicaris exoculata Williams & Rona, 1986 (MAR, 45°N–4°7S), Rimicaris kairei Watabe & Hashimoto, 2002 (Central Indian Ridge, Kairei and Edmond vent fields) and Rimicaris hybisae sp. nov. (Beebe and Von Damm vent fields, MCSC, Caribbean).

Rimicaris hybisae sp. nov. (Figures 1–7)

TYPE MATERIAL
Holotype: adult female, CL 15.3 mm. VDVF, MCSC, Caribbean Sea; co-ordinates: 18°22.605’N 81°47.875’W; water depth: 2300 m, [NHMUK 2011.8054]. Collected on the 44th voyage of RRS ‘James Cook’, on 18 April 2010.
Adult female, CL 10.8 mm; adult female with visible mature ovary, CL 7.0 mm; seven adult males, CL 7.0–11.8 mm; six juveniles, CL 3.6–6.7 mm. BVF, MCSC, Caribbean Sea;

Comparative Material Examined

**Chorocaris chacei** (Williams & Rona, 1986). Ten males, CL 9.7–13.0 mm [MNHN – Na17811]. MAR (Lucky Strike: Tour Eiffel; 37°17′N 32°17′W). Collected by net, 1689 m depth.

**Chorocaris vanouverae** Martin & Hessler, 1990. Paratypes: seven females, CL 8.0–12.6 mm [USNM 234947]. Mariana Back Arc Basin (Alice Spring Vent Field; 18° 12.599′N 144° 42.231′E). Collected by net, 3640 m depth.

**Rimicaris exoculata** Williams & Rona, 1986. Paratypes: ten females, CL 14.3–18.4 mm [USNM 228454]. Labelled as **Rimicaris chacei**; classified as **R. exoculata** juveniles at stage B by Komai & Segonzac (2008). MAR (TAG; 26° 08.3′N 44° 49.6′W). Collected by dredge, 2650–3620 m depth. Twenty-Four additional specimens: eleven males, CL 11.3–18.1: thirteen females, CL 8.8–18.4 mm from J. Copley’s reference collection. MAR (TAG).


**Opoapele loihi** Williams & Dobbs, 1995. Paratypes: twenty females, CL 8.0–11.7 mm [USNM 1005217]. North Pacific Ocean (Loihi Seamount; 18° 55′N 155° 16′W). Collected by baited traps, 990 m depth.

**Diagnosis**

Rostrum reduced to broadly rounded lobe, nearly reaching, reaching or slightly overreaching anterior margins of medially-fused eyes; ventral surface flat or slightly convex. Carapace and pleon with scattered minute setae; pleonlobal lobe broadly triangular or rounded; pterygostomial lobe rounded or blunt. Fourth pleonal pleuron posterolateral margin unarmored or armed with one tooth; produced into subacute posteroverentral angle. Fifth pleonal pleuron posterolateral margin unarmored or armed with 1–4 teeth; produced into acute posteroverentral angle. Sixth pleonal pleura 1.5–1.8 times longer than fifth in dorsal midline, 1.5 times longer than high; broadly notched for insertion of uropods; posterolateral process terminating in acute triangular tooth overlapping base of telson, posteroverentral corner subacute. Armature of pleonal sternites as described for **Chorocaris chacei** Williams & Rona, 1986.

**Telson** (Figure 3B, C) 1.5–1.7 times length of sixth pleonal pleura in dorsal midline, slightly narrowed posteriorly, length 2.2–2.9 times greatest width; posterior margin broadly convex, bearing row of 8–35 plumose setae and 2 spines at both lateral ends; 4–8 (sometimes asymmetrical) dorsolateral spines arranged in sinuous row.

Uropods (Figure 3B) with broad rami exceeding distal margin of telson; expod with distinct transverse suture and margins of fused eye-stalks; dorsal surface rounded, ventral surface flat or slightly convex. Carapace dorsal surface rounded; obsolete epigastric ridge present, broader than breadth between antennal lobes, defined by conspicuous grooves extending from bases of antennal lobes; ventral margin reinforced by low submarginal ridge, most robust and farthest from margin posteriorly. Antennal lobe rounded or broadly triangular, tip blunt or subacute; anterolateral margin between antennal lobe and pterygostomial expansion slightly convex. Pterygostomial expansion produced, exceeding antennal lobe, covering greater part of antennal basiscerite in larger specimens, rounded or blunt. Posterior submarginal groove present, poorly defined.

**Abdomen** (Figure 3A) evenly rounded dorsally, without carination; anterior three pleonal pleura unarmored marginally, posteroverentral angle rounded. Fourth pleonal pleuron posterolateral margin unarmored or armed with one tooth; produced into subacute posterioroverentral angle. Fifth pleonal pleuron posterolateral margin unarmored marginally or armed with 1–4 teeth; produced into acute posteroverentral angle. Sixth pleonal pleura 1.5–1.8 times longer than fifth in dorsal midline, 1.5 times longer than high; broadly notched for insertion of uropods; posterolateral process terminating in acute triangular tooth overlapping base of telson, posteroverentral corner subacute. Armature of pleonal sternites as described for **Chorocaris chacei** Williams & Rona, 1986.

**Rimicaris exoculata** (Williams & Rona, 1986). Ten males, CL 8.0–12.59 mm [USNM 243947]. Mariana Back Arc Basin (Alice Spring Vent Field; 18° 12.599′N 144° 42.31′E). Collected by net, 3640 m depth.


**Opoapele loihi** Williams & Dobbs, 1995. Paratypes: twenty females, CL 8.0–11.7 mm [USNM 1005217]. North Pacific Ocean (Loihi Seamount; 18° 55′N 155° 16′W). Collected by baited traps, 990 m depth.

**Diagnosis**

Rostrum reduced to broadly rounded lobe, nearly reaching, reaching or slightly overreaching anterior margins of medially-fused eyes; ventral surface flat or slightly convex. Carapace and pleon with scattered minute setae; pleonlobal lobe broadly triangular or rounded; pterygostomial lobe rounded or blunt. Fourth pleonal pleuron posterolateral margin unarmored or armed with one tooth; produced into subacute posteroverentral angle. Fifth pleonal pleuron posterolateral margin unarmored marginally or armed with 1–4 teeth; produced into acute posteroverentral angle. Antennae not operculiform; distolateral tooth first antennal peduncle subacute or blunt; antennal scale distolateral tooth subacute. Scaphognathite of maxilla and caridean lobe of first maxilliped bearing numerous plumose setae-like structures on dorsal and ventral surfaces; exopodal flagellum of first maxilliped completely reduced. Appendix masculina tapering distally with 7–8 spiniform setae restricted to tip. Uropodal protopod posterolateral projection triangular with acute tip.

In life, with four-lobed dorsal organ; lobes fused anteriorly; posterior lobes with paired ‘pores’ (Figure 1).

**Description**

Body integument smooth, firm, pitted with scattered, very shallow punctuations bearing minute scattered setae (including rostrum). Carapace (Figure 2) ovate–oblung, generally broader than deep in greatest dimensions (Table 2), distinctly broader than pleon; branchial regions distinctly inflated but to a lesser extent than that of **Rimicaris exoculata** Williams & Rona, 1986. Rostrum reduced to broadly rounded lobe; nearly reaching, reaching or slightly overreaching anterior...
two or three small spines at distolateral angle; endopod shorter and narrower than exopod; posterolateral projection of protopod triangular with acute tip.

Eye-stalks (Figure 2C) broadly fused mesially, lacking pigmentation, anterior surface without conspicuous tubercles.

Antennae (Figure 2) of normal structure. Antennular peduncles stout, dorsoventrally depressed, mesial surface rounded, not closely approximated; first and third segments nearly equal in length, second segment slightly longer; first segment with small distomesial tooth, strong distolateral tooth subacute or blunt, reaching or overreaching midlength of second segment, dorsal face convex; styllocerite moderately slender, lateral margin slightly convex, distinctly separated from first segment, extending beyond midlength of second segment; prominent proximolateral tubercle; second segment longer than broad or nearly as long as broad with small distomesial tooth. Antennular flagella robust, thick, extending mesially from base of tooth; plumose setae fringing in subacute tooth directed forward, short transverse suture extending mesially from base of tooth; plumose setae fringing broadly rounded distal margin and convex mesial margin.

Antennal basicerite bearing acute ventrolateral and ventromesial tooth.

Mouthparts (Figure 4) typical of Alvinocarididae. Mandible (Figure 4B) bearing 7 unequal acute teeth on mesial margin of broad incisor process (4 large and 3 small in holotype female), distalmost tooth distinctly separated from remaining teeth; molar process slightly upcurved, slender, unarmed, not reaching incisor; palp biarticulate, proximal article weakly curved, bearing 2 long plumose setae on distolateral margin, distal article stout, distinctly shorter than basal article, bearing numerous plumose setae of variable lengths on all margins and ventral face.

Maxillule (first maxilla) (Figure 4C) with both endites strongly curved toward mouth; coxal endite semitriangular, bearing long, dense, stiff setae; basial endite more rounded dorsally and distally, armed with row of stiff setae (shorter than those of coxal endite) and 3 rows of spines along mesial margin, each successive row becoming more regularly spaced, bearing spines in greater number and size; lateral margin bearing row of long plumose setae; palp weakly curved, slightly bilobed distally with proximal lobe bearing long plumose seta, distal lobe bearing short plumose seta.

Maxilla (second maxilla) (Figure 4D) with densely setose mesial endites; proximal endite curved, straplike lobe; distal endite composed of two lobes, separated from each other by a deep notch and suture; flanked by dorsoventrally compressed tapering palp; scaphognathite enormously expanded, numerous plumose setae like structures conspicuous on dorsal and ventral surfaces and lateral and mesial margins, supporting dense coverage of numerous filamentous bacteria-like structures (Figure 5); posterior lobe elongate, subtriangular, convex mesial margin distinctly notched, distomesial margin fringed with very long, wiry, tangled setae, preceded by much shorter plumose setae along proximomesial margin.

First maxilliped (Figure 4E, F) with irregularly fusiform, heavily setose mesial endite; palp concealed by caridean lobe, short and bilobed, proximal lobe straplike bearing plumose setae along margins, distal lobe triangular, without ornamentation; caridean lobe broad, similar in shape and ornamentation to scaphognathite, lacking flagellum; large epipod subrectangular, curving dorsally, scattered setae on distolateral margin only.

Second maxilliped (Figure 4G) composed of six segments as in other Alvinocarididae; coxa expanded mesially, bearing numerous plumose setae on mesial margin; merus and ischiobasis-fused segments moderately stout with numerous plumose setae on curved lateral surfaces, row of dorsally curved setae on nearly straight mesial surface; articulation between merus and carpus oblique; carpus short, long plumose setae on outer face; propodus with moderately long plumose setae mesially; articulation between propodus and dactylus oblique; dactylus longer than propodus, tapering to blunt distal margin, bearing very dense patch of short setae on mesial to distal margins forming brush-like structure; triangular epipod with slender rudimentary probotrbanch overreaching distal margin of epipod.

Third maxilliped (Figure 4H) overreaching antennal peduncle by one-third of ultimate segment, comprising coxa and three long segments; coxa heavily setose, with large, bilobed epipod; epipod without strap-like process; antepenultimate segment longest (consisting of fused basis–ischium–merus, but fusion between basis and ischiobasis incomplete with partial suture on dorsal surface and corresponding
indentations on lateral and mesial margins), dorsoventrally flattened, sinuously curved in dorsal view, armed with 1–2 spines at distolateral ventral angle, bearing numerous plumose setae on margins, dense cluster of long setulose setae on low elevation at proximomesial section, elevation length one-fifth of segment length, mesial margin notched where elevation terminates; penultimate segment with plumose setae on dorsolateral surfaces, rows of very dense, short, stiff setae on ventromesial face distal to one-third length; ultimate segment strongly curved, stout, about 1.5 times longer than penultimate segment, tapering distally to truncate tip bearing several terminal spines (7 on holotype female), trigonal in cross-section, lateral surface longitudinally carinate, with row of stiff setae, ventromesial surface flat with rows of very dense, short, stiff setae.

Branchial formula identical to that described in *Rimicaris* and *Chorocaris* (Williams & Rona, 1986; Williams, 1988; Martin & Hessler, 1990; Komai & Segonzac, 2008).
Pereopods (Figure 6) without epipods. First pereopod typical of family, polymorphic, smaller than succeeding pereopods, typically folded upon itself at mero-carpal joint, reaching tip of antennal peduncle when extended; carpus distal margin obliquely truncate for accommodation of proximal part of palm, mesial face bearing grooming apparatus (carpal brush sensu Martin et al., 1998: figures 1–3) comprised a triangular patch of serrate setae (some setules also serrate) arising from a recessed area, a row of distally-orientated serrate setae just proximal to the setal patch, and a stout spine proximal to the row of setae (Figure 5D); carpal brush setae bearing numerous filamentous and non-filamentous bacteria-like structures (Figure 5E, F); dactyl slightly overreaching fixed finger.

Second pereopod more slender than first, slightly twisted, just overreaching tip of antennal peduncle if extended; merus and ischium unarmed; carpus and chela much weaker than those of first pereopod.

Third to fifth pereopods similar in structure, moderately stout, normally folded at mero-carpal articulation, meri and carpi somewhat twisted, meri and ischia unarmed, decreasing in length from third to fifth (e.g. 20.5–18.0–17.1 mm respectively in holotype female); carpi 1.1–1.2 length of propodi in third pereopod, 0.9–1.1 in second, 0.7–0.9 in third; propodi increasing in length from third to fifth, with irregular double (more or less) row of spinules on ventral surface and normally 4 spinules on ventrodistal margin; dactyli subconical, 0.2 length of propodi, each terminating in robust, curved, corneous unguis, flexor surface bearing marginal and plantar rows of distally curved, corneous spinules, increasing in strength distally.
First pleopod bearing sexually dimorphic endopod; in female, endopod (Figure 6K) simple, terminating in blunt apex; in male, endopod (Figure 6L) with asymmetrical distal notch separating much produced mesial lobe from smaller distolateral lobe. Second pleopod with slender appendix interna without cincinnuli; appendix masculina (Figure 6M) (males) tapering distally, bearing 7–8 spiniform setae distally. Third and fourth pleopods each with slender appendix interna, third without cincinnuli, fourth bearing a few tiny cincinnuli at tip. Fifth pereopod with stout, more robust appendix interna with many cincinnuli in subapical mesial cluster.

**Coloration**

In life, carapace mostly pale translucent white; internal tissues neutral to greyish; integument of juveniles more translucent, oily orange globules visible underneath, tissues more orange.

Specimens from the BVF with rust-coloured deposits, most notably under antero-lateral area of carapace, on ventral
surfaces of thorax, abdomen, frontal region, all areas of maxilla and first maxilliped; blackening common under antero-dorsal area of carapace (Figure 1), on tips of dactyli, third maxilliped and carpal brush; black sparkly particles clustered between mouthparts. Specimens from the VDVF are all ‘clean’ in appearance, lacking the rust-coloured deposits, blackened areas and black particulate matter observed on specimens collected from the BVF.

Eyes lacking coloration and pigment; juveniles brown pigmentation present in proximal area of fused eyes; orange tint in smallest juveniles (CL 3.6–4.2 mm).

Four-lobed dorsal organ (Figure 1) highly reflective with a slight pink tint; reflective property and coloration not preserved in death or after chemical fixation; white pigmentation visible in specimens preserved in 100% ethanol; brown pigmentation under carapace in juveniles (where dorsal organ is located in adults).

Gills typically bright white.

Third to fifth pereopods each ending in pale brown dactylus visible in preservation.

**VARIATION**

Specimens from both vent fields exhibit similar morphology. Variation of some features within and between specimens, most notably the posterioroventral angle and armature of fourth and fifth pleonal pleura (Table 2), the number of dorso-lateral spines on the telson and distolateral spines on the exopod of the uropod (noted above). Slight intra- and interspecimen variation also observed in the degree of extension of the lateral lobe of the endopod of the first pleopod in males and the shape and reach of the distolateral tooth on the first antennal peduncle (noted above). Variability in these features does not appear to occur in any consistent combination, or in relation to sex or size.

The chela of the first pereopod appears to be polymorphic. In 16 specimens the chela of the first pereopod is slightly recurved, slender and somewhat delicate (Figure 6B). In contrast, one male (CL 5.1 mm), [NHMUK 2011.8066], BVF, has a stouter, more robust chela (Figure 6C).

No variation was observed between the female with a visible mature ovary (CL 7.0 mm) [NHMUK2011.8062] and other females.

One male specimen (CL 9.4 mm), [NHMUK 2011.8055] (Figure 7), from the VDVF has an acutely pointed rostrum, antennal lobe and pterygostomial expansion. All other specimens have a rounded or blunt antennal lobe and pterygostomial expansion with a rounded rostrum.

In juveniles (Table 2), carapace less inflated; rostrum distinctly pointed downwards, lateral and dorsal surfaces convex, anterior margin ornamented with small, distally-projecting setae; smallest juveniles (CL 3.6–4.2 mm) [NHMUK 2011.8067, NHMUK 2011.8068, NHMUK 2011.8070] medially-fused eyes with tiny tubercle on anterior surface medially.

Variation in coloration noted above.

**COMPARATIVE REMARKS**

The present new species has been mentioned previously in the literature as ‘a new morphospecies of alvinocaridid shrimp’ and ‘the MCSC vent shrimp’ (Connelly et al., in press) (Figures 4 & 5A). It is morphologically most similar to *Rimicaris exoculata*, *R. kairei* and *Chorocaris chacei* because of the reduction of the rostrum to a broadly rounded lobe and nonacuminate antennal lobe of the carapace, the presence of plumose-seta like structures on the dorsal and ventral surfaces of the scaphognathite of the maxilla and caridean lobe of the first maxilliped, and an appendix masculina armed with distal setae only. The new species is easily differentiated from *C. chacei* by the more inflated anterolateral region of the carapace, possession of a four-lobed dorsal organ, and acute tip of the uropodal podopod. A four-lobed dorsal organ and inflated carapace are known only for *R. hybisae* sp. nov. and the two other known *Rimicaris* species. The new species, however, is the first example within the genus to possess paired ‘pores’ on the posterior lobes of the dorsal organ. Furthermore, the carapaces of the new species and *R. exoculata* are ornamented with setae, whereas there are no setae on the carapace of *R. kairei*. The carapace of *R. hybisae* sp. nov. is slightly less inflated than that of *R. exoculata* and *R. kairei*. Of the three known *Rimicaris* species, the carapace is most strongly inflated in *R. kairei*. Other differentiating characters between *R. hybisae* sp. nov. and the two other *Rimicaris* species include the structure of the antennae and extent to which the eyes are fused and rostrum reduced. The characters differentiating between the new species and its closest relatives are discussed below.
DISTRIBUTION AND HABITAT
Known only from the type locality, the Von Damm (2300 m) and Beebe (4960 m) hydrothermal vent fields, Mid-Cayman Spreading Centre, Caribbean Sea. For preliminary descriptions of both vent fields, Connelly et al. (in press). Observed at the BVF in dense aggregations on the vent chimneys (>2000 individuals m⁻², Connelly et al., in press), and with high abundances of anemones around crevices issuing visible diffuse flow in the central area of the sulphide mound (Connelly et al., in press). At the VDFV, in dense aggregations around actively venting orifices of the edifice peak (>2000 individuals m⁻², Connelly et al., in press), along with another, numerically subordinate, morphotype of shrimp.

ETYMOLOGY
From the name of the British manoeuvrable TV grab HyBIS, in celebration of her first, and highly successful, scientific mission. The gender is feminine.

MOLECULAR PHYLOGENY
Partial sequences of the mitochondrial COI (460 bp) and 16S (549 bp) regions and the nuclear 18S (576 bp) region of Rimicaris hybisae sp. nov. were consistent among specimens from both sites. Unique and fixed mutations were observed in the partial sequences of the COI and 18S regions. Based on NJ and ML phylogenetic analyses for COI sequences available in GenBank, R. hybisae sp. nov. exhibits the smallest evolutionary distance to Alvinocaris sp. [AY163260.1], with a 1.96% divergence from this species, compared with a 7.39% divergence between R. hybisae and both R. exoculata and Chorocaris chacei. In the 16S region, no substitution was found between R. hybisae sp. nov. and C. chacei (0% divergence) based on the 300-bp sequence in GenBank for the latter species, whereas R. hybisae sp. nov. exhibits 0.47% divergence (424 bp) with R. exoculata. Phylogenetic analyses on the 300-bp region common among the species shows high bootstrap values (100% and 95% for NJ and ML methods respectively) separating the R. exoculata–R. hybisae sp. nov.–C. chacei clade from the other alvinocaridid species. Within this clade R. hybisae sp. nov. and C. chacei are separated from R. exoculata (88% bootstrap support, NJ and ML methods).

Fig. 8. Neighbour-joining tree of the Alvinocarididae based on a 540-base pair alignment of partial nucleotide sequences from the nuclear 18S ribosomal RNA region with Euganatonotus chacei Chan & Yu, 1991 (Nematocarcinidae) as an outgroup. Evolutionary distances computed using the Jukes–Cantor method (Jukes & Cantor, 1960) are represented by branch length; scale bar is proportional to inferred nucleotide divergence. Bootstrap support calculated on 100 re-sampling replicates is shown by the numbers along the branches (neighbour joining, roman text; maximum-likelihood, italic text). GenBank accession numbers are given after species names.

DISCUSSION
The presence of unique and fixed mutations in the partial sequences of the COI and 18S region suggest that Rimicaris hybisae sp. nov. is genetically distinct from all other species in the GenBank database. This supports the morphological evidence that R. hybisae is a new species. Although morphological variation was present amongst the specimens studied, partial sequences of the COI, 16S and 18S regions were consistent between specimens, confirming that those analysed from both MCSC vent fields are monospecific.

Based on morphology, and supported by the results from the molecular analyses, Rimicaris hybisae sp. nov. belongs within the Rimicaris–Chorocaris–Opaepele clade. Common features within this complex include a greatly reduced rostrum, broadly fused eyes, three or greater rows of accessory spines on the ventral surfaces of the dactyl of the third to fifth pereopods, the unarmed ischium of the third to fifth pereopods, and sinuous rows of dorsolateral spines on the telson (Komai & Segonzac, 2005, 2008). Rimicaris hybisae sp. nov. differs from Opaepele in possessing a more reduced rostrum, inflated carapace and non-acuminate antennal and pterygostomial lobes (Lunina & Vereshchaka, 2010). The assignment of the new species to a genus was a complex issue. Many morphological characteristics of Chorocaris are shared with Rimicaris (see Martin & Hessler, 1990; Komai & Segonzac, 2008), as exemplified by the original assignment of C. chacei to the genus Rimicaris by Williams & Rona (1986). However, a suite of morphological traits distinguish the two genera.

Two of the most striking morphological features of Rimicaris hybisae sp. nov. are its inflated carapace and four-lobed dorsal organ. These features are, to date, unique to R. hybisae longirostris Kikuchi & Ohta, 1995. Because there is only a single partial sequence in the database for both R. exoculata and C. chacei, it is not known if the mutations observed in the 18S partial sequences of these species are fixed within each of these species. Based on a 540-bp alignment, NJ and ML phylogenetic trees place R. hybisae sp. nov. in the same clade as R. exoculata and C. chacei (88% and 90% for NJ and ML methods respectively) (Figure 8). For the available 18S partial sequences the new species is closest in evolutionary distance to C. chacei (0.56% and 0.88% divergence with C. chacei and R. exoculata respectively).
Rimicaris and support placement of the new species within the genus. The carapace is marginally less inflated than that of *R. exoculata* (which is less inflated than that of *R. kairei* Watabe & Hashimoto, 2002 (authors, personal observation)). *Rimicaris hybisa* sp. nov. can be further distinguished from *R. exoculata* and *R. kairei* by the presence of paired ‘pores’ on the posterior lobes of the dorsal organ. Variability has been documented in the shape of the dorsal organ in adult specimens of *R. exoculata* (O’Neill et al., 1995: Figure 5), but the presence of ‘pores’ is, to our knowledge, a feature unique to *R. hybisa* sp. nov. The ‘dorsal eye’ of *R. exoculata* (and presumably *R. kairei*) is an extremely efficient photoreceptor, used for detecting light emitted from the vents (Pelli & Chamberlain, 1989; Van Dover et al., 1994, 1996; O’Neill et al., 1995). Shiny anterior spot-like organs have been described inside the carapaces of *Chorocaris chacei*, *Mirocaris fortunata* Martin & Christiansen, 1995, *Alvinocaridines formosa* Komai & Chan, 2010, and species of *Opaepele* and *Nautilocaris* Komai & Segonzac, 2004 (Desbruyères et al., 2006; Tsuchida et al., 2008; Komai & Chan, 2010). These spot-like organs may be homologous to the ‘dorsal eye’ found in species of *Rimicaris* (Kuenzler et al., 1997; Lakin et al., 1997; Komai & Chan, 2010), but are smaller and do not comprise four lobes. Histological examination of the dorsal organ, requiring the collection of further specimens, would be necessary to determine if a dorsal photoreceptor has coevolved in *R. hybisa* sp. nov.

Martin & Hessler (1990) hypothesized that *Rimicaris*, with its inflated carapace, opercular frontal region, dorsal organ, and dramatically reduced rostrum, is a derived genus that stemmed from *Chorocaris* or another morphologically similar deep-sea shrimp. The presence of an inflated carapace and four-lobed dorsal organ in *R. hybisa* sp. nov. suggest that this species may be more derived than species of *Chorocaris*. In contrast, the armature of the fourth and fifth pleonal pleura is a conservative feature, also found in more conservative genera (*Opaepele, Alvinocaris* and *Shinkaiocaris*: Komai & Segonzac, 2005; Komai et al., 2007). Within *Rimicaris* and *Chorocaris*, the fourth and fifth pleonal pleura are subacutely or acutely pointed only at their posterioventral angles and are not marginally armed (Komai & Segonzac, 2008).

Based on analyses of the COI gene (600 bp), Shank et al. (1999) proposed that *Chorocaris* is a paraphyletic assemblage with *C. chacei* being more closely related to *Rimicaris exoculata*. This is supported by the most recent and complete molecular phylogeny of the Alvinocarididae based on COI (600 bp), whereby *C. chacei* clusters with *R. exoculata* with strong statistical support (100% bootstrap values: Zelnio & Hureau, 2009). In *R. hybisa* sp. nov., *Rimicaris* species and *C. chacei*, the scaphognathite of the maxilla and caridean lobe of the first maxilliped are ornamented with numerous plumose-seta like structures on both their dorsal and ventral surfaces, whilst in *C. vandoverae* Martin & Hessler, 1990 and *C. paulina* Martin & Shank, 2005, their ventral surfaces are nearly naked (Martin & Hessler, 1990; Martin & Shank, 2005; Komai & Segonzac, 2008). The appendix masculina of *R. hybisa* sp. nov., *C. chacei* and the *Rimicaris* species bear distal setae only, whereas setae extend onto the dorsal surface of the appendix masculina in *C. vandoverae*. Komai & Segonzac (2008) suggest that this feature supports the close proximity between *C. chacei* and *Rimicaris* species and also consider *C. chacei* as a possible sister species of the *Rimicaris* clade. *Rimicaris hybisa* sp. nov., with shared morphological affinities with both *C. chacei* and *Rimicaris*, further supports the proximity between these taxa, although the more conservative features of the new species are not shared with either genus.

Features common to *Chorocaris* and absent in *Rimicaris exoculata* and *R. kairei* include: possession of a strong distotateral tooth, a small distomesial tooth, and a prominent proximolateral tubercle on the first segment of the antenna peduncle; a clear separation of the styllocerite from the antennal peduncle; a carpal brush on the first pereopod; the armed antepenultimate segment of the third maxilliped; blunt or subacute antennal teeth; an increase in length from the third to fifth pereopods and a well-developed, functional appendix interna bearing cincnuli on the fifth pereopod only (Martin & Hessler, 1990; Komai & Segonzac, 2008; authors, personal observation). These traits are also exhibited by *R. hybisa* sp. nov., revealing some morphological affinities with the genus *Chorocaris*.

Notable autapomorphies of *Rimicaris* are: the complete fusion of the eyes into a transverse ocular plate; the reduction of the rostrum to a broadly rounded lobe, fitting closely to the posterior concavity of the ocular plate; the formation of the antennal components into an operculum-like structure and the presence of a mat of dense spinules on the flexor surface of the propodi of the third to fifth pereopods (Martin & Hessler, 1990; Komai & Segonzac, 2008). These features were not observed in *R. hybisa* sp. nov., despite the examination of specimens comparable in size to adult *R. exoculata* and *R. kairei*.

In consideration of the morphological and molecular evidence presented here, it appears that *Rimicaris hybisa* sp. nov. may be intermediate between *Chorocaris chacei* and *R. exoculata*. Given the uncertainty concerning the *Chorocaris* genus, the establishment of a new genus for *R. hybisa* sp. nov. is premature. In reverence to the fact that *C. chacei* was originally *Rimicaris chacei*, the assignment of *R. hybisa* sp. nov. to the genus *Rimicaris* is the most conservative approach available. As Komai & Segonzac (2008) have already suggested, a comprehensive and extensive molecular phylogenetic analysis of the whole *Rimicaris – Chorocaris – Opaepele* clade is required to clarify the relationships between these taxa. Such a study has the potential to improve markedly our current understanding of the evolution, radiation and biogeographical patterns of these shrimp among deep-sea chemosynthetic environments in the world’s oceans.

Morphological variation is well documented in the Alvinocarididae and is acknowledged as common within alvinocaridid species (e.g. Kikuchi & Ohta, 1995; Martin & Shank, 2005; Komai & Segonzac, 2008). The variation described between specimens of *Rimicaris hybisa* sp. nov. does not appear to be related to size, gender, or collection site. Polyomorphism of the chela of the first pereopod has also been described for species of *Chorocaris* (Martin & Shank, 2005; Komai & Segonzac, 2008). Specimens of *C. chacei* from Lucky Strike (one female in Komai & Segonzac, 2006: Plate 3, p. 241; one male in Komai & Segonzac, 2008: figure 9F, G) have been shown with an acutely pointed rostrum, antennal lobe and pterygostomial expansion; these specimens were considered by Komai & Segonzac (2008) to be an aberrant form of the species, and although this identification may not be fully justified, it is reasonable given the sampling location. Consequently the specimen illustrated in Figure 7
Komai & Segonzac (2008) noted differences in the morcarpal brush on the first pereopod. In a recent review, tooth on the first segment of the antennal peduncle and a Chorocaris chacei by the more inflated anterolateral region Rimicaris chacei acute tip of the uropodal protopod. Like juveniles of C. of the carapace, possession of a four-lobed dorsal organ, and is closest in evolutionary distance to Rimicaris hybisae sp. nov. is easily differentiated from Chorocaris chacei, although this is based on a 576-bp alignment only.

Rimicaris hybisae sp. nov. is readily distinguished from Chorocaris chacei by the more inflated anterolateral region of the carapace, possession of a four-lobed dorsal organ, and acute tip of the uropodal protopod. Like juveniles of C. chacei, juveniles of R. hybisae sp. nov. bear plumose setae on the posterior margin of the telson, a conspicuous distolateral tooth on the first segment of the antennal peduncle and a carpal brush on the first pereopod. In a recent review, Komai & Segonzac (2008) noted differences in the morphology of ovigerous females in species of Chorocaris and Rimicaris. Samples of ovigerous females of R. hybisae sp. nov. are required to enable their morphology to be described and compared to other species.

In summary, morphological features and molecular analyses indicate that Rimicaris hybisae sp. nov. belongs within the Rimicaris–Chorocaris–Opaepele clade, closest to and intermediate between C. chacei and R. exoculata. The inflated carapace and four-lobed dorsal organ of R. hybisae sp. nov. are diagnostic and distinguishing morphological features, previously recorded only in R. exoculata and R. kairei, which support placement of the new species within the genus Rimicaris. The molecular evidence reported here confirms that R. hybisae sp. nov. is a genetically distinct species, closest to C. chacei, which was originally placed in the genus Rimicaris as R. chacei (Williams & Rona, 1986). Phylogenies of the Alvinocarididae suggest that Chorocaris is polyphyletic, with C. chacei more closely related to Rimicaris than to other Chorocaris species (Shank et al., 1999; Zelnio & Hourdez, 2009). Moreover, on the basis of morphological traits shared between the two taxa, it has been proposed that C. chacei is a sister species of Rimicaris (Komai & Segonzac, 2008). The most conservative approach is therefore to expand the diagnosis of Rimicaris to incorporate R. hybisae sp. nov., rather than to erect a new genus in the absence of highly corroborated phylogeny. The presence of features previously considered diagnostic of Rimicaris spp. and C. chacei in R. hybisae sp. nov., and the low genetic divergence between these taxa suggest that reassimilation of C. chacei within Rimicaris could also be considered in the future.

### Biogeography

Rimicaris hybisae sp. nov. represents the third named species in the genus, all of which are known only from hydrothermal vents in a particular area (Table 1).

Rimicaris karei is so far restricted to its type locality in the Indian Ocean, whereas R. exoculata is present at vents along the MAR, where it occurs sympatrically with Chorocaris chacei (Table 1). Rimicaris hybisae sp. nov. extends the distribution of the genus approximately 4000 km westwards into the Caribbean and increases the bathymetric range of the Alvinocarididae by 872 m to 4960 m. This may also be the first record of the Alvinocarididae in the Caribbean. Escobar-Briones & Villalobos Hiriart (2003) reported an indeterminate species of Alvinocaris from non-chemosynthetic environments on the Banco Chinchorro, northern Caribbean, at depths of 176–203 m but provided no molecular evidence or catalogue details.

Before the complete closure of the Isthmus of Panama by 3.1 Ma (Burton et al., 1997), a deep-water connection existed between the eastern Pacific and Caribbean. Martin & Hessler (1990) proposed that the presence of Chorocaris species in the Atlantic and Pacific indicates a faunal connection between the eastern Pacific and Mid-Atlantic vents. However, no specimens of Rimicaris have been collected from the Pacific Ocean, despite numerous active surveys at Pacific vents. In addition, Chorocaris may be paraphyletic, with the Atlantic species (C. chacei) belonging to Rimicaris. The recent discovery of hydrothermal vents and chemosynthetic communities on the MCSC provides an opportunity to test Martin & Hessler’s (1990) hypothesis. The presence of shrimp-dominated communities at the BVF and the VDF also indicate that the MCSC vent fauna shares similarities with MAR vent fauna. The descriptions of other novel taxa at MCSC vents (Nye et al., unpublished data) will further elucidate the factors determining vent biogeography of this region.

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REFERENCES


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