**CHOROCARIS VANDOVERAE, A NEW GENUS AND SPECIES OF HYDROTHERMAL VENT SHRIMP (CRUSTACEA, DECAPODA, BRESIILIIDAe) FROM THE WESTERN PACIFIC**

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**ABSTRACT.** A new genus and species of bresiliid shrimp, *Chorocaris vandoverae*, is described from hydrothermal vents in the Mariana Back-Arc Basin, a spreading center in the western Pacific. The genus is morphologically close to *Rimicaris*, a genus known from vents along the north Mid-Atlantic Ridge. Characters that distinguish *Chorocaris* from *Rimicaris* include a third maxilliped composed of three (rather than four) long segments, a more concave pterygostomial border of the carapace, and a wide, blunt rostrum. The two genera differ also in the morphology of the orbital region, antennae, and third maxilliped. In *Rimicaris*, the antennal area is slightly opercular, meeting the branchiostegal border and covering the mouthparts, whereas this region is normal in *Chorocaris*. *Rimicaris chacei* is transferred to *Chorocaris*, leaving *Rimicaris exoculata* the sole species in *Rimicaris*. The discovery of *Chorocaris* in the western Pacific, in conjunction with other recent finds of Pacific and Atlantic vent species, indicates a possible faunal connection between western Pacific and Mid-Atlantic vent areas. A key to the currently accepted genera of the Bresiliidae is included.

**INTRODUCTION**

Two genera of caridean shrimp have been previously reported from the vicinity of marine hydrothermal vents. The genus *Alvinocaris* was erected by Williams and Chace (1982) to accommodate *A. lusca*, an unusual bresiliid shrimp from thermal vents of the Galapagos Rift. Characters of *Alvinocaris* were such that the family Bresiliidae, already recognized by most workers as an unnatural assemblage, had to be slightly redefined and expanded to accommodate the new genus (Williams and Chace, 1982). Three additional species of *Alvinocaris* were later reported from the Atlantic and Gulf of Mexico (Williams, 1988). The genus *Rimicaris* was erected by Williams and Rona (1986) to accommodate two new species of the Bresiliidae from hydrothermal vents along the Mid-Atlantic Ridge at 26°N. Additional Mid-Atlantic Ridge records (23°22′N) for the two species of *Rimicaris* were reported by Williams (1987), and the genus received popular attention when it was discovered that one of the two species, *R. exoculata* Williams and Rona, 1986, has, in lieu of normal eyes, a pair of large organs just below the cuticle of the cephalothorax. These organs contain rhodopsin and apparently function in light perception (Van Dover et al., 1989; Pelli and Chamberlain, 1989).

A. B. Williams (personal communication) was aware at the time of the original description of *Rimicaris* that the two species (*R. exoculata* and *R. chacei*) differed in many respects, but because the available material was rather limited, and because the two species shared many characters, he refrained from erecting a second genus for *R. chacei*. The present paper is based on a relatively large collection of shrimp from hydrothermal vents along the Mariana Back-Arc Spreading Center in the western Pacific. This new material has allowed us to describe a new genus and species of the Bresiliidae and to reconsider the generic placement of *R. chacei* Williams and Rona, 1986, which is herein transferred to our new genus, *Chorocaris*. The number of known bresiliids is raised to nine genera and 17 species.

**METHODS AND MATERIALS**

Shrimp were collected during a series of dives with the submarine *Alvin* in April and May, 1987. The collection sites consisted of three active vent fields along the spreading center of the Mariana Back-Arc Basin at about 18°N, just west of the Mariana Island Arc, at depths of 3595–3660 m (Hessler et al., 1988; Hessler and Martin, 1989). The shrimp, which lived in profusion at vent openings or in the immediately adjacent rocks, were collected with
nets manipulated by the mechanical arm of the submarine. Most of the shrimp were fixed in 4% buffered formalin and stored in 80% ethanol. Others were frozen for physiological analyses. Drawings were made with a Wild M5APO dissecting stereoscope with camera lucida. Morphological comparisons were facilitated by the following clearing and staining protocol. Specimens were macerated in warm potassium hydroxide, rinsed with water, and stained with aqueous aniline blue before stepwise dehydration in ethanol. Alcoholic specimens (in absolute ethanol) were then transferred to Terpineol®, a commercially available mixture of oils that is slightly miscible with water, maintains flexibility of specimens, and greatly enhances visibility of cuticular structures.

SYSTEMATICS

Chorocaris new genus

Rimicaris Williams and Rona, 1986:447 (in part; R. chacei only).

DIAGNOSIS. Carapace smooth, spineless, pterygostomial margin slightly concave. Rostrum wide and blunt, unarmed, nearly reaching or exceeding postorbital prominences in length. Eyestalks cylindrical, fused medially, lacking pigment in adults. Antenna 2 scale broadly oval, with distinct notch on distolateral border. Mandible with 2-segmented palp, distinct separation between incisor and molar processes. Second maxilla with scaphognathite greatly expanded anteriorly and conspicuously setose. First maxilliped with greatly expanded exopod, similar to scaphognathite. Second maxilliped with merus and ischium short, stout, as wide or wider than dactylus. Third maxilliped composed of 3 long segments and 2 shorter basal segments. Telson with 6–9 pairs of submarginal dorsal spines and usually 2 pairs of posterolateral spines. Branchial formula as in Rimicaris and Alvinocaris (see Williams, 1988). Male anatomy not known.

TYPE-SPECIES. Chorocaris vandoverae, new species.

ADDITIONAL SPECIES. Rimicaris chacei Williams and Rona, 1986.

ETYMOLOGY. From the Greek words choros (dance) and karis (shrimp), in reference to the rapid, active, demersal behavior of these shrimp. The gender is feminine.

Chorocaris vandoverae new species

Figures 1, 2, 3a–e

MATERIAL. 119 adults, all apparently females, from the following dives:

Dive 1835, 26 April 1987, Snail Pits portion of Burke vent field, 3660 m, 18°10.948’N, 144°43.204’E, 37 shrimp (4 missing).

Dive 1836, 27 April 1987, Burke vent field (both Snail Pits and Anemone Heaven portions), 3660 m, 18°10.917–18°10.948’N, 144°43.210–144°43.204’E, 42 shrimp (35 frozen).

Dive 1837, 28 April 1987, Burke Field, 3660 m, 18°10.0’N, 144°43.2’E, 10 shrimp (all frozen).

Dive 1843, 4 May 1987, Alice Springs vent field, 3640 m, 18°12.599’N, 144°42.431’E, 30 shrimp (1 of which was dissected and used for illustrations herein).

TYPE MATERIAL. Holotype female, Dive 1843, National Museum of Natural History, Smithsonian Institution, USNM 243946. Designated paratypes have been deposited in the National Museum of Natural History (10 females, Dive 1843, USNM 243947); the Natural History Museum of Los Angeles County, Los Angeles, California (12 females, Dive 1835, LACM 87-272.1; 7 females, Dive 1836, LACM 87-273.1; 7 females [1 dissected], Dive 1843, LACM 87-274.1); and the Muséum National d’Histoire Naturelle, Paris, France (10 females, Dive 1843, MNHN-NA 11924). All additional material (i.e., not designated paratype) listed above is in the Scripps Institution of Oceanography, La Jolla, California.

Several specimens that were not examined in preparing the description, but that are almost certainly this species because they were taken from the same collections, are in the personal collections of R.R. Hessler, C.L. Van Dover, S. Ohta, and the Emperor of Japan.

MEASUREMENTS. Carapace length (CL) from 5.7 to 15 mm, total length (TL) from 16.3 to 52 mm (N = 34); holotype CL 15 mm, TL 52 mm.

DIAGNOSIS. Rostrum clearly exceeding anterior-most projection of postorbital prominence. First pereiopod with distomedial carpal cleaning brush.

DESCRIPTION

CARAPACE (Figs. 1a–d). Smooth, with minute scattered setae. Not laterally inflated (compare to Rimicaris). Frontal dorsal border produced into blunt rostrum that exceeds acute postorbital prominences (Fig. 1d, arrow). Anterolateral (pterygostomial) border slightly concave between ventrolateral projection and postorbital prominence. Ventrolateral projection extending anteriorly beyond level of rostrum. Slight groove extending posterolaterally

Figure 1. Chorocaris vandoverae, female paratype from LACM 87-274.1: carapace, antennae, abdomen, and uropods. a, Entire animal, lateral view; b, dorsal view of carapace and bases of antennae; c, frontal region of carapace, lateral view, eyestalks removed; d, dorsal view of frontal region of carapace and eyes, arrow indicating acute postorbital prominence; e, left first antenna peduncle, ventral view; f, left antennal scale, dorsal view; g, left antennal scale and antennal peduncle, ventral view; h, telson and uropods. All figures except b from the same individual. Scale bar = 10.0 mm for a, b; 5.0 mm for c–g; 6.5 mm for h.
Figure 2. *Chorocaris vandoverae*, female paratype from LACM 87-274.1: pereiopods. a, Cheliped, dorsomedial view; b, “inner” view of chela; c, second pereiopod; d, chela of second pereiopod; e-g, third through fifth pereiopods; h, i, lateral and posterior views (respectively) of dactylus of third pereiopod. Scale bar = 5.0 mm for a, c, and e-g; 1.25 mm for all others.
Figure 3. *Chorocaris vandoverae*, female paratype from LACM 87-274.1 (a-e); *Chorocaris chacei*, female paratype LACM 85-174.1 (f, g); and *Rimicaris exoculata*, female paratype LACM 85-174.2 (h); selected mouthparts. *Chorocaris vandoverae*: a, left mandible, “outer” view; b, first maxilla; c, second maxilliped; d, third maxilliped, right side, ventral view; e, tip of terminal segment of third maxilliped. *Chorocaris chacei*: f, third maxilliped, ventral view, penultimate segment appearing shorter because of bend toward viewer; g, distal segment of third maxilliped. *Rimicaris exoculata*: h, third maxilliped, ventral view. Scale bar = 5.0 mm for d and h, 1.25 mm for a, b, c, and g; 2.5 mm for c and f.
from lateral border of each postorbital prominence. Dorsal surface immediately posterior to lateral extent of each eyestalk with ill-defined pigmented areas running longitudinally; carapace otherwise uniformly off-white.

**EYES (Figs. 1a, d).** Reduced, just visible in dorsal view between rostrum and postorbital prominences, with few setae on anterior surface of non-faceted cornea. Pigment lacking, except slight pigmentation in lateral extremity of eyestalk in some juveniles. Eyestalks cylindrical, fused and contiguous medially (Fig. 1d).

**ANTENNAE.** Antenna 1 peduncle (Fig. 1c) with obvious tooth on ventral surface of basal segment and sharp anteriorly directed spine or tooth distolaterally. Stylocerite acute, extending almost to distal border of second peduncular segment, slightly concave mesially. Antenna 2 (Figs. 1b, f, g) with oval scale bearing slight notch at distal third of mesial border; dorsally with slight central longitudinal ridge; ventrally as shown (Fig. 1g).

**PEREIOPODS.** Cheliped (Figs. 2a, b) stout, slightly twisted, with distinct carpal brush and with chela strongly curved inward; proximal dorsal border of propodus with groove just distal to articulation with carpus; fingers of chela fringed with small teeth, obvious on dactylus but minute and nearly undetectable on propodus; fixed finger twice length of palm. Second pereiopod (Figs. 2c, d) chelate, dactylus about length of propodus; fingers armed with even row of small teeth, larger distally. Third through fifth pereiopods (Figs. 2e-i) achelate and similar, with short dactylus bearing basal tooth and several sharp, curved spines on posterior surface.

**MOUTHPARTS.** Mandible (Fig. 3a) with 6–7 similarly sized teeth on incisor process; palp 2 segmented, both segments with long setae. Maxilla 1 (Fig. 3b) with 2 stout setae and several smaller setae on endopod as shown in figure. Maxilla 2 and first maxilliped (not illustrated) hypertrophied and roughly similar to those of *Rimicaris exoculata* and *R. (now Chorocaris) chacei* (Williams and Rona, 1986). Maxilliped 2 (Fig. 3c) stout, segments wide, dactylus longer than propodus and slightly curved upward distally. Maxilliped 3 (Figs. 3d, e) composed of 3 long segments, the terminal segment possibly representing a fused dactylus and propodus; most proximal of 3 long segments strongly curved.

**BRANCHIAE.** As described for the genus *Rimicaris* by Williams and Rona (1986) and further described for both *Rimicaris* and *Atrimicaris* by Williams (1988).

**ABDOMEN (Figs. 1a, h).** Posterolateral angles of abdominal somites 4–6 becoming sharper posteriorly; somite 2 with greatly expanded pleura as wide or wider than height of carapace, posterolateral margin rounded; somite 3 with posterolateral angle rounded. Telson (Fig. 1h) with 7–9 pairs of spines on dorsal border, number occasionally differing from side to side; posterior border with 2 pairs of posterolateral spines, inner pair longer; outer branch of uropod with 2 stout spines on external (lateral) border of diuresis.

**PLEOPODS (not illustrated).** Similar to those illustrated by Williams and Rona (1986) for *Rimicaris chacei*.

**ETYMOLOGY.** We are pleased to name this species for Cindy Lee Van Dover in recognition of her stimulating contributions to the biology of hydrothermal vent decapods.

**COMPARATIVE MORPHOLOGY OF RIMICARIS AND CHOROCARIS**

**ORTAL REGION**

*Rimicaris exoculata* was originally described as lacking any eyes (Williams and Rona, 1986). Although it is true that the typical cylindrical eyestalk seen in other caridean shrimp is lacking, we believe that the eyestalk is present but is greatly reduced and modified. This is best illustrated by comparing the derived genus *Rimicaris* with the relatively primitive *Chorocaris*. In *Chorocaris* the eyestalks are medially fused, so that in dorsal or frontal views the fused stalks appear as a single transverse cylinder. In dorsal view the mediolateral portion of this cylinder is concealed by the rostrum, although in cleared specimens (see Methods and Materials) the entire cylinder is apparent in dorsal view (Fig. 1d). If the rostrum is missing, or markedly reduced as in *Rimicaris*, then the fused eyestalks are readily visible. The flattened transverse plate in the orbital area of *Rimicaris exoculata* is, we believe, just a further modification of the transverse, nonfunctional, fused eyestalk seen in *Chorocaris*. This condition was suspected by Williams and Rona (1986) and is indicated in their terming this greatly modified eyestalk the transverse ocular plate. We have labeled this flattened eyestalk op (for ocular plate) in Figures 4a and 4b.

**FRONTAL REGION**

The frontal region of *Rimicaris exoculata* is unique among all known caridean shrimp. The stylocerite of the first antenna and the scaphocerite of the second antenna are both very broad and flat. This in itself is not unusual, but these plates also fit tightly against one another and against the other antennal components of the frontal region, all of which are also flattened, with the result being an opercular plate-like shielding of the mouthparts. The opercular effect is facilitated by a lateral, basal projection of the first antenna peduncle that slightly exceeds the lateral extension of the base of the scaphocerite. This rather blunt projection, visible in the ventral view of the antennal peduncle given by Williams and Rona (1986:452, fig. 6a), creates a slot between itself and the ventral surface of the scaphocerite blade. The slot accommodates the upper pterygostomial border of the carapace, and the resulting fit of the carapace border into this slot enhances the opercular nature of the frontal region.
of the shrimp (Figs. 4a–d, heavy arrow). The expanded frontal region of the shrimp thus shields the mouthparts dorsally. The greatly inflated carapace is distended to the point that the anteroventral borders nearly touch each other ventrally, thus shielding the mouthparts to a lesser degree ventrally as well. Williams and Rona (1986:452) noted that all legs and even the antennal flagellum "are capable of being placed under [the] branchiostegite." The dorsal surface of the scaphocerite is also modified, bearing a longitudinal ridge (rs, Figs. 4b, c) that serves to close the gap between the scaphocerite
and the segments of the peduncle of the first antenna.

In both species of Chorocaris, the frontal region is normal, i.e., there is no tendency for the antennal components to appear or function as an operculum, although a slight longitudinal ridge is present on the scaphocerite (see Fig. 1f). The reason for this modification in R. exoculata is unknown.

MAXILLIPEDS

The third maxilliped of Rimicaris is composed of four long segments and one or two fused, shorter, basal segments. In contrast, in both species of Chorocaris the third maxilliped is composed of only three long segments and two short basal segments. The most proximal of the long segments in Chorocaris probably can be equated with the proximal long segment in Rimicaris, as the curvature and general shape is very similar (Figs. 3d-h). It is more difficult to decide which of the more distal segments in Rimicaris are the homologues of those in Chorocaris. The third maxilliped of C. chacei was illustrated as having four segments by Williams and Rona (1986, figs. 9i, j). On closer examination, it appears that the maxilliped is composed of only three long segments, with the distal-most segment slightly constricted at about ⅔ its length.

The second maxilliped also differs markedly between Rimicaris exoculata and the two species of Chorocaris. In R. exoculata, this maxilliped is thin, with the merus and ischium elongate and strongly concave along their medial margins (see Williams and Rona, 1986, fig. 6h; Van Dover et al., 1988, figs. 2C, 3). In Chorocaris the second maxilliped is much more robust and is at most only slightly concave along the mesial borders of the merus and ischium.

DISCUSSION

SYSTEMATICS

Many characters of Chorocaris are shared with Rimicaris, and this is of course reflected in the original assignment of C. chacei and R. exoculata to the same genus (Rimicaris) by Williams and Rona (1986). Of the characters that we feel are of generic importance, all except one (the reduction in segmentation of the third maxilliped) are probably plesiomorphic; i.e., they are shared by several other bresiliid genera and species. Thus, we feel that Rimicaris, with its inflated carapace, opercular frontal region, dorsal "eyespots," and lack of a rostrum, is clearly a derived genus that stemmed from Chorocaris or some other morphologically similar deep-sea shrimp. The establishment of Chorocaris necessitates modifying the diagnosis of Rimicaris, as it originally included a species (R. chacei) that we transfer to Chorocaris. Additionally, we think it is possible that the eyestalks in Rimicaris exoculata are reduced, flattened, and nonpigmented, rather than absent (Figs. 4a, b). The modifications to the Williams and Rona (1986) diagnosis of Rimicaris, which now is monotypic, are as follows.

Rimicaris, Emended Diagnosis

Carapace greatly inflated laterally. Pterygostomial margin convex. Rostrum absent; median frontal region of carapace greatly recessed. Eyes lacking pigment, eyestalks flattened, completely fused medi ally, visible in dorsal view. Antennal scale broadly oval with margin smooth, lacking dorsal distolateral notch or groove. Antennal scale, bases of antennae, and stylocerite closely approximated, forming opercular complex shielding mouthparts; antennal scale bearing dorsal ridge closing gap between scale and stylocerite. Mandible with 2-segmented palp, distinct separation between incisor and molar processes. Second maxilla with scaphognathite greatly expanded anteriorly and conspicuously setose. First maxilliped with greatly expanded exopod, similar to scaphognathite. Third maxilliped with 4 long and 2 short segments. Second maxilliped with merus and ischium extremely narrow, less than width of dactylus, with strongly concave medial border.

There are several other characters that separate Rimicaris exoculata from species in Chorocaris, but we hesitate to include these as characters of generic importance. These include the following character states in Rimicaris: Stylocerite fused to most of lateral margin of podomere (fused only to basal ⅓ of podomere in both species of Chorocaris); tip of stylocerite reaching or just exceeding distal end of podomere 2 (short of that in Chorocaris); podomeres of antenna relatively slender (stout in Chorocaris); cheliped lacking carpal cleaning brush (see Bauer, 1981) (cheliped with carpal brush in C. vandoverae and to a lesser extent in C. chacei).

The more slender second maxilliped of Rimicaris as compared with Chorocaris, a difference noted in the above modifications to the diagnosis of Rimicaris, is more easily seen in studies of the feeding appendages (see Williams and Rona, 1986, fig. 6h; Van Dover et al., 1988, fig. 2C).

The two species of Chorocaris are rather easy to distinguish. The rostrum is more pronounced in C. vandoverae, clearly exceeding the postorbital prominences, whereas in C. chacei the rostrum reaches or barely exceeds these prominences. This difference is even more pronounced in juveniles, where the postorbital prominences are clearly defined in C. vandoverae but barely discernable in C. chacei. Other differences include a more slender stylocerite and the presence of a larger carpal cleaning brush (Bauer, 1981) in C. vandoverae. One difference that might be assumed from the original illustrations of C. chacei (as Rimicaris chacei) is that the cheliped is more stout, with the finger being only about half the length of the palm. However, in the paratype of R. chacei that we examined (one female, Natural History Museum of Los Angeles County, LACM 85-174.1), the cheliped is essentially identical to that seen in R. exoculata and C.
vandoverae, leading us to believe that the cheliped of the animal figured by Williams and Rona (1986, figs. 10a–c) is perhaps aberrant.

It is interesting to note that no males have been collected for either species of Chorocaris, although males were described for Rmicus exoculata by Williams and Rona (1986). Males of R. exoculata differ only slightly from females; the endopod of the second pleopod bears a distal notch, and the second pleopod bears an appendix masculina (Williams and Rona, 1986).

With the descriptions of Alvinocaris, Rimicaris, and now Chorocaris, it is becoming increasingly apparent that the family Bresiliidae is an artificial assemblage. The range of characters exhibited by the nine genera (Bresilia Calman, 1896; Discias Rathbun, 1902; Lucaya Chace, 1939; Pseudocheles Chace and Brown, 1978; Tridiscias Kelsey, 1983; Alvinocaris Williams and Chace, 1982; Rimicaris Williams and Rona, 1986; Encantada Wicksten, 1989; and Chorocaris) presently constituting the Bresiliidae (including the former Disciadidae; see Forest, 1977; Forest and Cals, 1977; Chace and Brown, 1978; Williams and Chace, 1982; Williams and Rona, 1986; Williams, 1988) is great, and there is no single character that uniquely defines the group. We think it likely that the group is comprised of several monotypic or low-diversity families. Until such time as a family-wide revision is undertaken, we follow the lead of other workers by expanding once again the limits of the Bresiliidae and incorporating Chorocaris into the key to the bresiliid genera below (modified after Williams and Rona, 1986).

Biogeographic Implications

In our earlier paper on Mariana vent crabs (Hessler and Martin, 1989) we refrained from discussing biogeographical implications of the western Pacific vent fauna because so little was known at that time. The discovery of Chorocaris adds to a growing body of evidence that there is a faunal connection between the Mariana vent area and the northern Mid-Atlantic Ridge. As unlikely as this may seem,
we cite the following evidences in support of the theory. The genus *Chorocaris* is known from these two areas only. A more conservative taxonomic approach, placing our new species in *Rimicaris*, would not eliminate the disjunct distribution, as the genus *Rimicaris* would then be represented in these two areas only. Second, as we mentioned briefly in our paper on vent crabs (Hessler and Martin, 1989), the Mariana vent crab (*Austroagraea williamsi*) appears morphologically most similar to *Segonzacia mesatlantica* (Williams, 1988) (formerly *Bythograea*; see Guinot, 1989) from vents along the Mid-Atlantic Ridge. The pattern occurs also in mollusks. The limpet genus *Pseudorhithula* McLean, erected for the western Pacific vent species *P. marianaec* McLean, 1989, has now been collected from vents along the Mid-Atlantic Ridge (McLean, 1989; James McLean, personal communication, 1989), and a new genus of mussel is known from the Mid-Atlantic and western Pacific only (Grasse, 1989). There are active vents south of the Mariana area. Deep-sea taws in the north Fiji Basin have resulted in photographs of what are undoubtably bythograeid crabs and galatheid lobsters from vent sites (Honza and Auzende, 1988), and a second species of *Austroagraea* Hessler and Martin, 1989, has been collected from deep waters near the Tonga Islands (Daniele Guinot, personal communication, 1989).

We propose that the hydrothermal areas of the western Pacific and northern Mid-Atlantic were at one time connected via a series of active vent areas, not necessarily active simultaneously, that extended from the Mid-Atlantic Ridge south to the Atlantic-Indian Ocean Ridge, north along the Southwest Indian Ocean Ridge, Mid-Indian Ocean Ridge, and Southeast Indian Ocean Ridge, and finally north through the various spreading centers of the Indo-West Pacific. There is insufficient evidence for us to hypothesize what direction this faunal interchange might have taken. It should also be noted that at least one species of limpet occurs in both the Mariana and East Pacific/Galapagos vent areas but as yet is not known from the Atlantic (James McLean, personal communication, 1989). Elucidation of the origins and distributions of vent faunas will likely prove a complex problem.

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