

Comparison of the Carpal Cleaning Brush in Two Genera of Hydrothermal Vent Shrimp (Crustacea, Decapoda, Bresiliidae)

JOEL W. MARTIN,* JAMES SIGNOROVITCH, AND HEMA PATEL
Natural History Museum of Los Angeles County, Los Angeles, California

ABSTRACT Clusters of specialized serrate setae in patches called "carpal cleaning brushes," or carpal-propodal brushes, are found on the distal margins of the chelipedal carpus in many species of caridean shrimps and other decapod crustaceans. These brushes, used to clean the antennal flagellum, occur in some bresiliid shrimp species associated with hydrothermal vents in the Pacific and Atlantic oceans, and recently their presence has been proposed as a distinguishing taxonomic character at the genus level. Occurrence of such brushes in shrimp that live near hydrothermal vents is of interest because of the high number of bacteria associated with these vents. These shrimp have the potential to be heavily fouled with bacteria, whereas at the same time preliminary studies suggest that they may depend upon these bacteria at least in part (or possibly exclusively) for food. We employ scanning electron microscopy to examine and describe the general morphology and location of carpal brushes on the chelipeds of all known species in two vent shrimp genera, *Rimicaris* Williams and Rona and *Chorocaris* Martin and Hessler. The brush is well developed and clearly delimited in all known species of *Chorocaris*, where it consists of a triangular field of serrate setae and a posterior blunt spine that possibly functions as a "stop" to keep the antennal flagellum in place during grooming. *Rimicaris exoculata* has no recognizable carpal cleaning brush or any serrate setae on the chelipedal carpus and thus appears derived relative to species of *Chorocaris* with regard to this feature. A newly described species, *R. aurantiaca*, is somewhat intermediate, having no carpal brush but with two serrate setae and a blunt spine in the region occupied by the brush in species of *Chorocaris*. Possible implications and comparisons to the genera *Alvinocaris* and *Opapaele* are discussed briefly. *J. Morphol.* 235:31-39, 1998. © 1998 Wiley-Liss, Inc.

Cleaning and grooming mechanisms and morphology in caridean shrimps and other decapod crustaceans have been fairly well documented (see reviews in Bauer, '81, '89). Carideans may employ several appendages to clean themselves, but use primarily the third maxillipeds, chelipeds, and the tips of the walking legs to groom the general body surface, gills, embryos, antennae, and antennules. Grooming is a time- and energy-consuming activity that is important to the shrimp's survival. Bauer ('75, '77, '79) has shown that amputation of cleaning appendages sometimes results in extreme fouling of the body and its other appendages; shrimps prevented from grooming their antennules become severely fouled and even suffer loss of olfactory setae. As noted by Bauer ('81,

'89), grooming structures also may have value in decapod systematics and phylogeny, although they have been employed for that purpose only rarely. The carpal brush of the cheliped, or carpal-propodal brush if found on the adjoining surfaces of both the carpus

Contract grant sponsor: National Science Foundation (to K. Wise and S. Lafferty); Contract grant number: ESI 9552406, in support of the Museum Research Apprentice Program of the Natural History Museum of Los Angeles County; Contract grant sponsor: Research Experiences for Undergraduates award (to J.W.M.); Contract grant number: DEB 9642010, supplemental to DEB 9320397.

J. Signorovitch is now at 5153 N. Campus #5, Cornell University, Ithaca, NY 14853.

H. Patel is now at 2171 Albright Ave., Upland, CA 91784.

*Correspondence to: Joel W. Martin, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

and propodus, consists of a field of specialized serrate setae that function in cleaning the shrimps' antennal flagellum (Bauer, '75, '78, '81). The flagellum is drawn slowly through the slightly bent cheliped at the carpal-propodal joint, and any fouling materials are removed by the dense array of serrate setae (e.g., Bauer, '78, Fig. 4 for three species of caridean shrimp; Bauer, '89, Fig. 3 for the stenopodid *Stenopus hispidus*, Fig. 8D-F for the caridean *Leander tenuicornis*, and Fig. 9D-F for the caridean *Heptacarpus pictus*).

Some of the most conspicuous faunal components of the hydrothermal vent fields of the Mid-Atlantic Ridge are the large numbers of caridean shrimps in the genera *Rimicaris*, *Chorocaris*, and (to a lesser degree) *Alvinocaris*. The occurrence of carpal brushes in shrimp inhabiting vent fields is of particular interest. Most known hydrothermal vent sites are characterized by the presence of high numbers of chemosynthetic bacteria. Indeed, these bacteria support, either directly or indirectly, the unusual communities of life found at these vents (e.g., Grassle, '86; Tunnicliffe, '91; Casanova et al., '93; Wirsén et al., '93; Van Dover, '95). Yet there is also the possibility that bacterial fouling poses a larger problem for vent species than it would for species in other marine habitats; indeed, vent shrimp are known to harbor large numbers of bacteria on various parts of the appendages and body surface (Casanova et al., '93). Although descriptions of the chelipeds of these shrimp usually contain some illustrations and/or verbal accounts of the carpal cleaning brush, these have never been examined in any detail. Recently, Martin et al. ('97) use the presence of the carpal brush to distinguish between two genera of bresiliid shrimps from hydrothermal vents, *Rimicaris* (as modified by Martin et al., '97) and *Chorocaris*, which together contain five species to date. The present study is a comparison of the details of the carpal cleaning brush in these two most prevalent shrimp genera of the Mid-Atlantic Ridge hydrothermal vent fields, using shrimp from these sites and also species of *Chorocaris* from vent sites in the western Pacific.

MATERIALS AND METHODS

Shrimp were collected by various researchers on expeditions to the Mariana Back-Arc Basin Spreading Center in the Pacific (see Hessler et al., '88; Hessler and Martin, '89; Martin and Hessler, '90) and to the TAG,

Lucky Strike, and Snake Pit hydrothermal vent sites of the Mid-Atlantic Ridge (see Segonzac, '92; Van Dover, '95; Nuckley et al., '96, and individual species treatments below). Abbreviations used in measurements are CL for carapace length, CW for carapace width, and TL for total length; the abbreviation LACM indicates the catalog number in the Crustacea collections at the Natural History Museum of Los Angeles County. Drawings were made with the use of a Wild M5APO dissecting stereoscope and a Nikon Labophot compound binocular microscope. Preparation for scanning electron microscopy involved hydration to pure water, brief sonication in a Branson^c Model 1200 ultrasonicator with minute amounts of a commercial surfactant (Branson^c GP Formulated Cleaning Concentrate) added to distilled water as the sonication fluid, dehydration through a graded ethanol series, drying via hexamethyldisilazane (HMDS) (Nation, '83), and sputter coating with gold prior to examination with a Cambridge 360 Stereoscan at an accelerating voltage of 10kV at the Center for Electron Microscopy and Microanalysis on the University of Southern California campus. Materials used are described below.

Genus *Chorocaris* (Martin and Hessler, '90)

Chorocaris chacei (Williams and Rona, '86).

Two chelipeds from same specimen, CL = 19.0 mm, CW = 11.1, TL = ~57.6 mm, collected 2 June 1993, Lucky Strike hydrothermal vent, Mid-Atlantic Ridge, *DSRV Alvin* Dive 2607 (donated by S. Chamberlain, Syracuse University).

Chorocaris vandoverae (Martin and Hessler, '90). Two chelipeds from same specimen, Paratype, LACM 87-272.1, claws removed only (body remains with other paratypes) from individual measuring CL = 8.9 mm, CW = 4.6 mm, TL = 25.1 mm, collected 26 April 1987, Snail Pit, Burke Vent Field, Mariana Back-Arc Spreading Center, 3660 m, *DSRV Alvin* Dive 1835.

Chorocaris fortunata (Martin and Christiansen, '95). Two chelipeds removed from same individual, Paratype, LACM 95-45.3, claws removed only (body remains with other paratypes) from individual measuring CL = 7.3 mm, CW = 3.2 mm, TL = ~22.6 mm, collected 2 June 1993, Lucky Strike hydrothermal vent, Site 3, 1624 m, *DSRV Alvin* Dive 2607.

Genus *Rimicaris* (Williams and Rona, '86).

Rimicaris exoculata (Williams and Rona, '86). Both chelae removed from individual measuring CL = 16.7 mm, CW = 12.0 mm, TL = 40.8 mm, collected 24 June 1993, Snake Pit hydrothermal vent field, *RV Atlantis II* cruise 129-7, *DSRV Alvin* Dive 2623 (donated by R. Jinks and S. Chamberlain, Syracuse University).

Rimicaris aurantiaca (Martin et al., '97). Two specimens from paratype series, LACM 93-46.2, measurements for larger specimen CL = 10.1 mm, CW = 5.4 mm, TL = 26.7 mm; for smaller specimen CL = 9.5 mm, CW = 5.2 mm, TL = 26.1 mm, collected 19 June 1993, Snake Pit Hydrothermal Vent Field (Moose vent [l'Elan] site), Mid-Atlantic Ridge, *R/V Atlantis II* cruise 129-7, *DSRV Alvin* Dive 2618, 3520 m (see Nuckley et al., '96; Martin et al., '97).

RESULTS

Genus *Chorocaris*

Chorocaris chacei (Figs. 1a,b, 2a,b)

The carpus of the *Chorocaris chacei* cheliped bears a well-developed, triangular field of serrate setae, with one apex of the triangle directed proximally such that the widest part of the field is adjacent to the rounded posterior "heel" of the inflated chelipedal "hand" (propodus) (Fig. 1a, b). Setae on the periphery of the brush are slightly shorter than those located more centrally. Each seta arises from a well-defined, circular socket (see also description of *C. vandoverae* below, and Figs. 1c, e, 2d). Each seta is proximally cylindrical, becoming distally flattened, and is serrate along two borders on the distal half to two-thirds of the setal shaft (shown in Fig. 1d for *C. vandoverae*). Each setule arises from a poorly developed "socket" on the setal shaft (i.e., with crescent-shape indentations on either side of the setule, but without a continuous circular socket), and the setules are themselves minutely serrulate as well. The tip of the seta is distinct from the main setal shaft, with shorter setules that are not serrulate and that form a slightly spatulate tip directed toward the chelipedal propodus (as shown in Fig. 1c,d for *C. vandoverae*).

Just proximal to the triangular field of serrate setae is a stout, simple spine arising from a socket (Figs. 1b, e, Fig. 2a white arrow). This spine appears to mark the posterior terminus of the carpal cleaning brush and possibly functions as a "stop" to keep the antennal flagellum in place as it is pulled

along the carpal cleaning brush during bouts of grooming. A "stop" on the carpal brush may be needed because of the absence of any propodal brush, which in other shrimp "are usually somewhat more setose and may be the principal scraping or rasping structure" (Bauer, '89, p. 54).

Chorocaris vandoverae (Figs. 1c-e, 2c,d)

Features exactly as for *Chorocaris chacei*, but with one significant difference. In *Chorocaris vandoverae* there is a pair of serrate setae on the opposing surface of the chelipedal propodus (Fig. 2c, black arrow in Fig. 2d), much as is seen in previous descriptions of some non-vent caridean shrimp (e.g., Bauer, '75, '78). There is also a row of shorter, nonserrate setae along the medial border of the brush region (not actually part of the brush). It is possible that this row is present also in *C. chacei*, but the specimens of *C. chacei*, we examined were more heavily fouled (Fig. 2a, b), and this area was obscured. In the specimens of *C. vandoverae* examined by us, accidental loss of setae (by oversonicating) allowed us to count the actual number of setae in the field; there were ~46 on the left cheliped (Fig. 2d) and 49 on the right (not figured).

The stout, simple spine at the proximal terminus of the carpal brush occurs in the same area (Fig. 1e, 2c white arrow) as described for *Chorocaris chacei*.

Chorocaris fortunata (Fig. 2e,f)

Chelipeds are similar to those of both *Chorocaris chacei* and *Chorocaris vandoverae*, but with the entire field of setae slightly depressed, arising from a recessed area of cuticle (Fig. 2e, f). Details of the individual setae (i.e., socket, shaft, setules, tip) are as described for *C. chacei* and *C. vandoverae* above. There are additional differences in the nature of the cheliped that do not involve the cleaning brush, but that may be important in terms of grooming. Although not mentioned or illustrated in the original description by Martin and Christiansen ('95), the outer surface of the chelipedal fingers bear long, curved, gently sweeping setae that are minutely serrulate and comblike along almost the entire length of the seta. The fingers of the cheliped are themselves minutely pectinate, as is the case for all other known vent-inhabiting bresiliid species, but this pectination is in some ways obscured by the setal rows (Fig. 2e). The bases of these setae typically are covered by

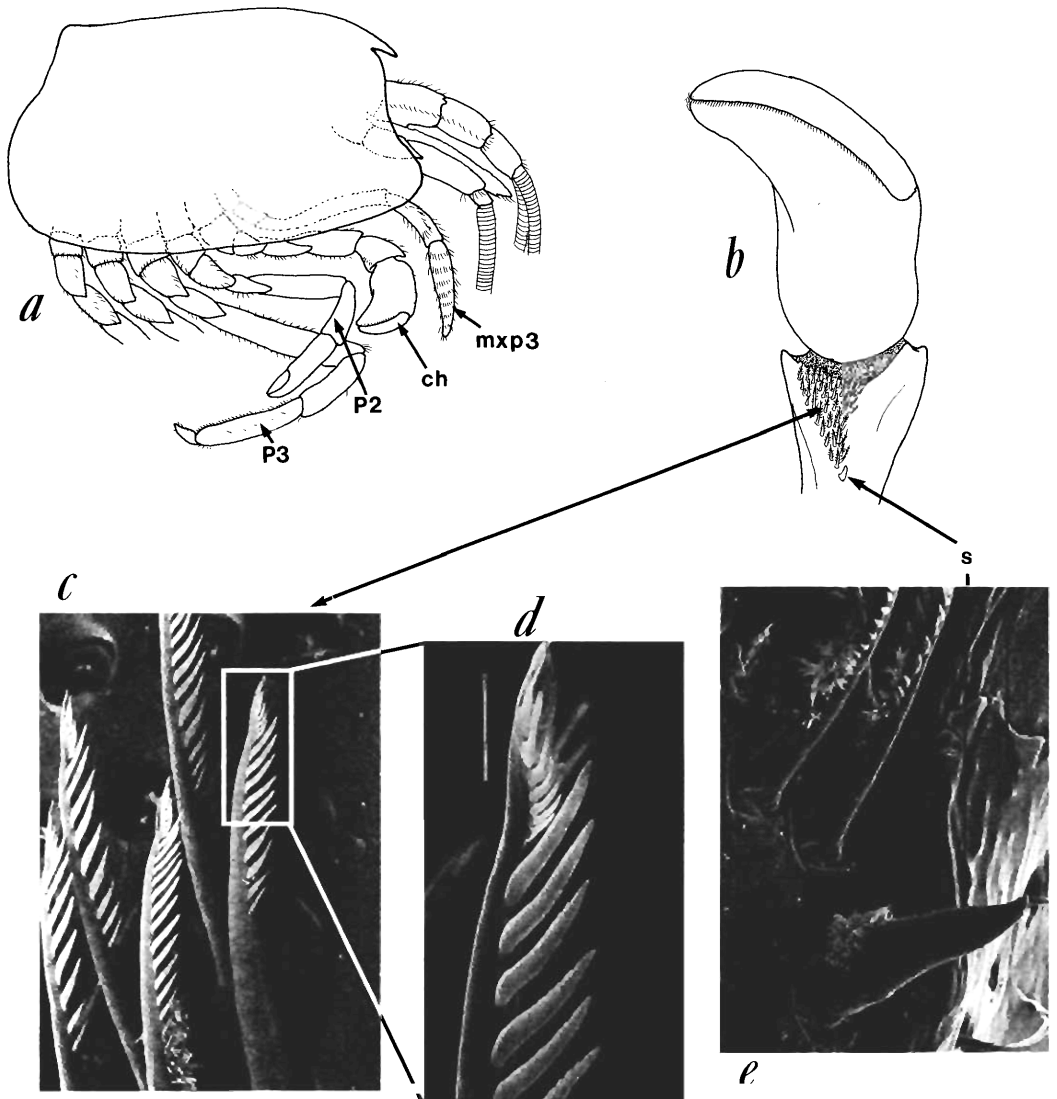


Fig. 1. Schematic view of the cheliped and the carpal cleaning brush in vent-inhabiting shrimp. The figure is somewhat artificial in that (a) and (b) are based on *Chorocaris chacei*, whereas (c), (d) and (e) are scanning electron micrographs of the carpal brush of *C. vandoverae*. (a) carapace and pereopods of *C. chacei*, lateral view, with third maxilliped, cheliped (first pereopod),

second pereopod, and third pereopod labeled. (b) chela and part of the carpus of *C. chacei* showing location of carpal cleaning brush. (c and d) scanning electron micrographs of the cleaning setae. (e) The blunt spine (s) that marks the posterior terminus of the carpal cleaning brush. (a) is redrawn from Segonzac et al. ('93). Scale bars = 50 μ m for (c) and (e); 20 μ m for (d).

dense accumulations of small rod-shaped bacteria. Although not part of the carpal brush, these long comblike setae almost certainly play some role in scraping, but whether for grooming or for feeding purposes is not known.

The stout, simple spine at the proximal terminus of the carpal brush occurs in the

same area (Fig. 2e white arrow) as described above for both *Chorocaris chacei* and *Chorocaris vandoverae*.

Genus *Rimicaris* *Rimicaris exoculata* (Fig. 3a,b)

The carpus, which is longer relative to the chela than in species of *Chorocaris*, lacks a

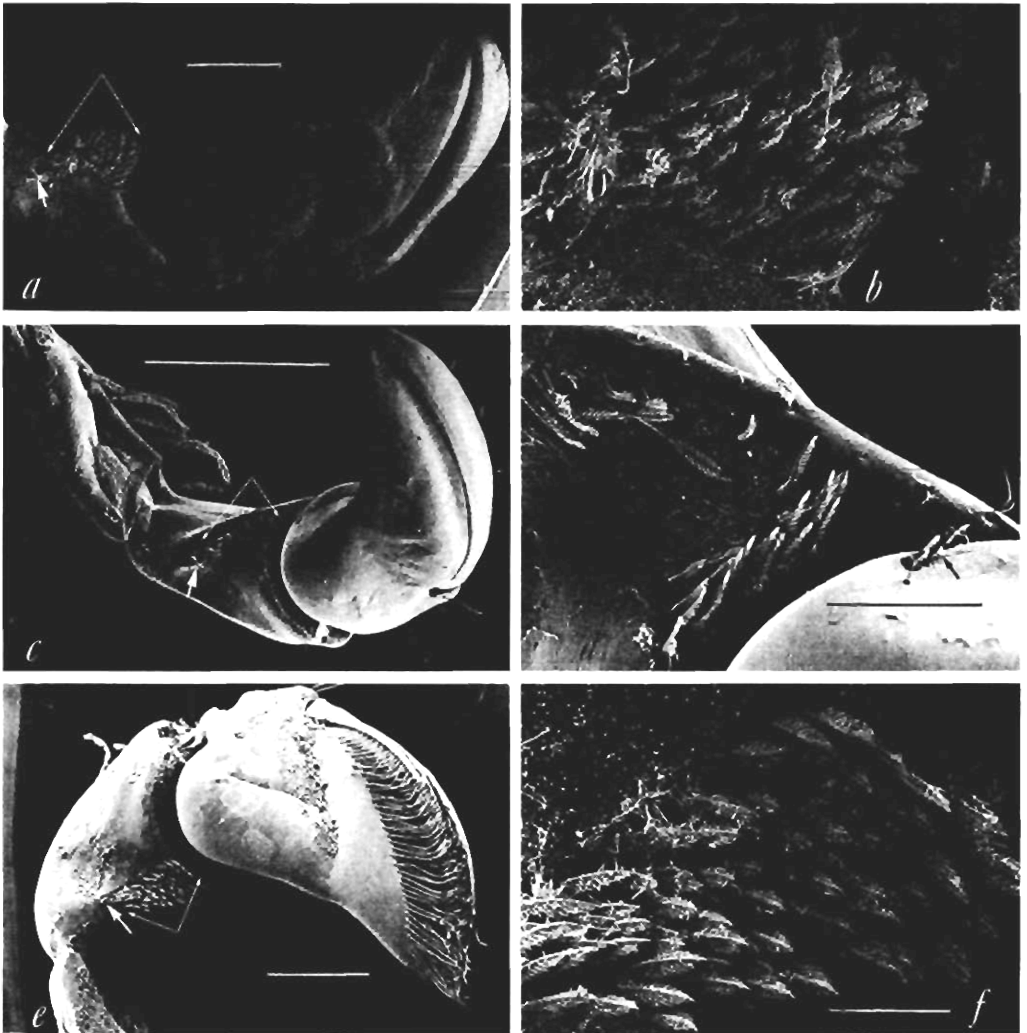


Fig. 2. Scanning electron micrographs of the three distal articles of the cheliped (a, c, e) and higher magnifications of the carpal cleaning brush (b, d, f) in species of *Chorocaris*. (a, b) *Chorocaris chacei*, Lucky Strike hydrothermal vent site, Mid-Atlantic Ridge. (c, d) *Chorocaris vandoverae*, Mariana Back-Arc Basin, western Pacific. (e, f) *Chorocaris fortunata*, Lucky Strike vent site,

Mid-Atlantic Ridge. Thin white arrows in (a), (c), and (e) indicate extent of carpal cleaning brush. Thick white arrows on (a), (c), and (e) point to posterior terminal spine at proximal end of carpal brush. Black arrow in (d) indicates serrate setae of the propodus. Scale bars = 1.0 mm for (a and c), 0.5 mm for (e), 200 μ m for (b and d), 100 μ m for (f).

field of serrate setae. No individual serrate setae were found on any area of the carpus or the propodus (Fig. 3a, b). No stout, simple spine was found on the carpus. In this regard our findings agree with those of Van Dover et al. ('78).

Rimicaris aurantiaca (Fig. 3c,d)

There is no true "carpal cleaning brush" as is seen in any of the species of *Chorocaris*.

However, two setae, details of which are almost exactly as described above for *Chorocaris* species, are borne on the distal border of the carpus (Fig. 3c, d). These appear shorter and are perhaps less spatulate on the tip than the setae described for *Chorocaris*, although this may be a size-related difference only. A stout, simple spine (Fig. 3c, d, white arrow) arising from a circular socket, exactly as is found in *Chorocaris* species,

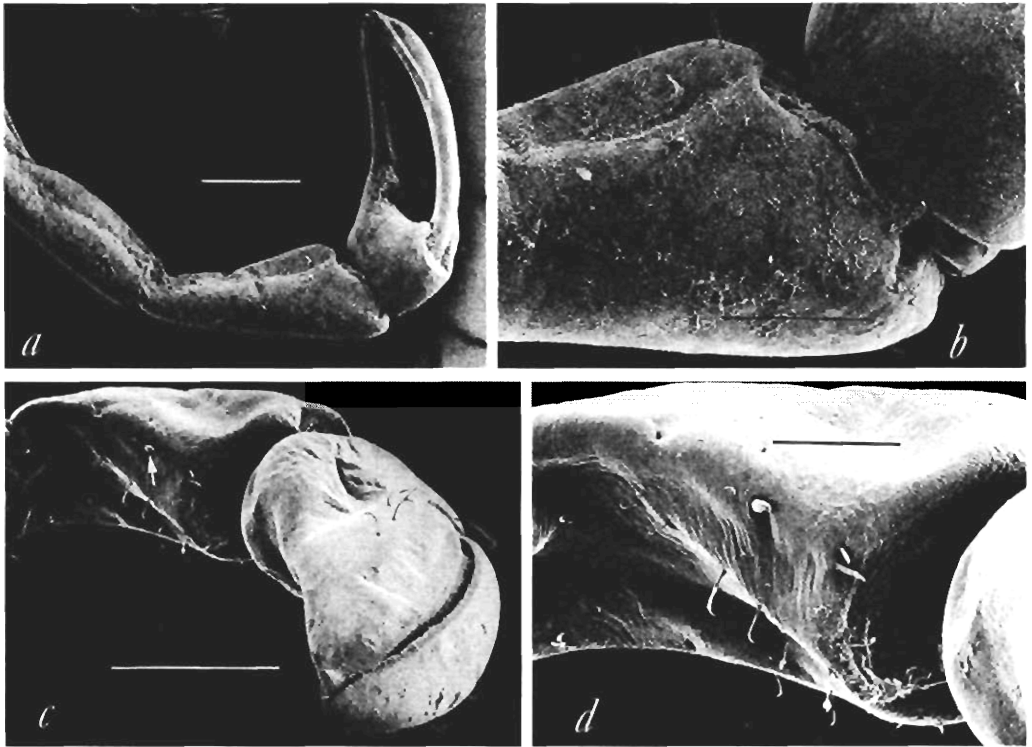


Fig. 3. Scanning electron micrographs of the distal three articles of the cheliped (a, c) and higher magnifications of the region where the carpal cleaning brush is found in other carideans (b, d) in species of *Rimicaris*. (a, b) *Rimicaris exoculata*, Snake Pit hydrothermal vent

site, Mid-Atlantic Ridge. (c, d) *Rimicaris aurantiaca*, Snake Pit hydrothermal vent site, Mid-Atlantic Ridge. White arrow in (c) indicates posterior terminal spine, shown at higher magnification in (d). Scale bars = 1.0 mm for (a), 0.5 mm for (b and c), 200 μ m for (d).

occurs proximal to this pair of setae, with only smooth unarmed cuticle in between. The row of simple, nonserrate setae just medial to the carpal brush described above for *C. vandoverae* also is present (along an oblique line from upper left to lower right in Fig. 3d because of different orientation of cheliped).

DISCUSSION

Carpal cleaning brush in hydrothermal vent shrimp

The presence and nature of the carpal brush differs between species of *Chorocaris* and *Rimicaris*, supporting placement by Martin et al. ('97) of the recently described *R. aurantiaca* in the genus *Rimicaris*. However, this difference is not as great, nor is it as clear-cut, as we had earlier believed (Martin et al., '97). Although *R. aurantiaca* lacks a true carpal cleaning brush in the traditional sense of that term (e.g., Bauer, '81), the presence of the two serrate setae and the

stout posterior spine are highly suggestive of a condition not far derived from what is seen in species of *Chorocaris*. Indeed, the presence of the blunt posterior spine would argue for uniting them, as this has not been described in other bresiliid species (vent or nonvent) to date. Martin et al. ('97) commented on the fact that *Rimicaris aurantiaca* "in many ways bridges the morphological gap between the genera *Rimicaris* and *Chorocaris*," and Segonzac et al. ('93, p. 563, addendum) had noted earlier the "occurrence at the Snake Pit [hydrothermal vent field] of a new species with features intermediate between *Rimicaris exoculata* and *Chorocaris chacei*" (from the English translation). This morphologically intermediate position of *R. aurantiaca* is further evidenced in the present work. We can easily envision a transformation series from a "normal" caridean shrimp, possessing typical frontal compound eyes, a carpal-propodal cleaning brush, and a well-developed rostrum,

through *Chorocaris*, with its reduced rostrum, carpal (but not carpal-propodal) brush, and frontal optical array, to finally *Rimicaris*, species of which lack a brush altogether, have lost the rostrum (except in *R. auran-tiaca*), and have a bizarre dorsally oriented optical complex (see Van Dover et al., '89; O'Neil et al., '95; Nuckley et al., '96; Kuenzler et al., '97).

The other two genera of bresiliid shrimp described from hydrothermal vents have species with eyestalks that appear more "typical" (although the function is completely different from that described for surface-dwelling shrimp, at least in *Alvinocaris*) (see Wharton et al., '97), well-developed rostrums, and well-developed carpal cleaning brushes. We base this comparison on the descriptions and illustrations of Williams and Chace ('82), Williams ('88), and Segonzac et al. ('93) for species of *Alvinocaris*, and of Williams and Dobbs ('95) for *Opapaele*, a fourth genus of vent-inhabiting Bresiliidae that to date consists of a single species, *O. loihi*, found on the Loihi Seamount off Hawaii (Williams and Dobbs, '95). Although these authors do not always refer to the carpal cleaning brush as such, it is usually mentioned. Williams and Chace ('82, p. 143) mention the "heavily setose" surface between the lateral and mesial ridges of the chelipedal carpus of *Alvinocaris lusca*, and Williams and Dobbs ('95, p. 231) refer to the carpus of *O. loihi* as having a "patch of setae," which is almost undoubtedly a carpal cleaning brush based on its location (their Fig. 2c). The carpal brush is clearly illustrated for all three species of *Alvinocaris* described by Williams ('88), and in one of the scanning electron micrographs in that work (Williams, '88, p. 276, Fig. 7f) the carpal brush can be seen at lower right, where it appears to originate in a depressed region similar to that described above for *Chorocaris fortunata*. Thus, *Alvinocaris* and *Opapaele* are less derived than are species of either *Chorocaris* and *Rimicaris* based on the above characters (rostrum, eyes, carpal brush). Because SEM has been used only sparingly in descriptions of vent shrimp (e.g., Williams, '88; Van Dover et al., '88; Martin et al., '97), details of the carpal brush, such as the nature of the individual setae and the presence or absence of the stout spine at the posterior terminus of the field, are unknown.

Among other (nonvent) bresiliids, it is unclear whether a carpal brush exists. If the

carpal brush as described here does not exist in other bresiliids, then its presence in vent species might support Christoffersen's ('86) recognition of the family Alvinocarididae (see also Segonzac et al., '93). We are not aware of any descriptions or illustrations of the carpal cleaning brush in other bresiliids, but our assumption is that it has been overlooked or not recognized as a cleaning brush. Wicksten ('89), e.g., describes the carpus of *Encantada spinocolata*, a species that is morphologically close to the *Bresilia-Alvinocaris-Rimicaris-Chorocaris* group of bresiliids (Williams and Rona, '86; Wicksten, '89), as having a "tuft of setae at [the] articulation with [the] chela," and this may be a carpal brush. In addition, Forest and Cals ('77) illustrated what is probably a carpal-propodal brush in their description of a second species of *Bresilia*, *B. corsicana* (Forest and Cals, '77, p. 557, Fig. 13), describing the carpus (p. 556) as having "*une rangee antero-ventrale de soies raides, plumeuses*." It would be interesting to compare the details of the carpal brush setae and spines in species of all genera currently treated as bresiliids to see if this character helps resolve the issue of whether the vent-inhabiting bresiliids should be recognized as a separate family, the Alvinocarididae, as proposed by Christoffersen ('86, '91), or retained in the Bresiliidae (e.g., see Chace, '92; Holthuis '93; see also discussions in Segonzac et al., '93; Williams and Dobbs, '95; Martin and Christiansen, '95).

Need for a carpal cleaning brush in vent shrimp

The propensity for hard surfaces in marine environments to become fouled rather quickly would argue for the need for cleaning mechanisms in all marine decapod Crustacea (Bauer, '75, '89). At hydrothermal vents, the potential for fouling would seem even greater than in other marine habitats, because these shrimp live near, and apparently feed on, enormous populations of microbes (Van Dover et al., '88; Gebruk et al., '93; Segonzac et al., '93; Casanova et al., '93). Furthermore, the antennal flagellum is clearly of vital importance to vent-inhabiting shrimp. Renninger et al. ('95) have shown that species of *Rimicaris* can detect, and are attracted to, sulfides, specifically N_2S , and that this geochemical sensory ability allows them to locate vent sites. Renninger et al. ('95) also demonstrated that it is the antennular and antennal sensory setae that serve

as the detectors. The need to keep these appendages unfouled is therefore obvious and critical (see also Bauer, '89, section 6.1). The absence of a carpal brush in species of *Rimicaris* is thus somewhat puzzling. It may be that *Rimicaris* relies on other appendages to clean its antennal flagellum. Many carideans use the third maxillipeds for this purpose, and in fact Bauer ('77, p. 261) called grooming with these appendages "a characteristic behavior of caridean shrimp and other decapods," and later (Bauer, '79, p. 70) noted that "the P1-C1 carpal brushes are not essential to antennal grooming and that their function is easily supplied by the third maxillipeds." Of the 15 caridean families surveyed by Bauer ('78), a survey that did not include the Bresiliidae, 13 had a carpal-propodal brush. Alpheids and atyids apparently employ the third maxilliped alone for this task. Of course, the chelipeds in these two families (Alpheidae, Atyidae) are rather highly specialized, which does not appear to be the case for the vent-inhabiting bresiliids. Better stated, if the vent shrimp chelipeds are more specialized than those of non-vent bresiliids, it is not yet known for what purpose(s). One interpretation of having a carpal brush in *Chorocaris* alone is that either the cheliped of *Rimicaris* is in some way more specialized than it is in species of *Chorocaris*, or at least is used in other ways, and/or that *Rimicaris* employs other appendages to clean the antennal flagella. If *Rimicaris* species use the third maxilliped to groom the antennal flagellum, it would seem well suited for the task, as it bears, in both species, rows of variously armed spines and setae (see especially Figs. 5a, b of *R. aurantiaca* in Martin et al., '97). Comparison of the details of the third maxilliped in species of *Rimicaris* and *Chorocaris* and also in the other vent-inhabiting bresiliids would seem a worthwhile endeavor.

ACKNOWLEDGMENTS

We thank the staff of the Education Branch of the Natural History Museum, especially S. Lafferty and J. Trochez, and the other participants in the MRAP program, as well as Todd Zimmerman, George Davis, and Karen Wise in the museum's Research and Collections Branch, for their assistance, support, and encouragement. We also thank Alicia Thompson for her help with the SEM component of the study, and Cindy Lee Van Dover, S.C. Chamberlain, and R.N. Jinks for providing some of the specimens upon which

this report is based. Finally, we thank R.T. Bauer for commenting on the manuscript.

LITERATURE CITED

- Bauer, R.T. (1975) Grooming behaviour and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae). *Zool. J. Linn. Soc.* 56:45-71.
- Bauer, R.T. (1977) Antifouling adaptations of marine shrimp (Crustacea: Decapoda: Caridea): functional morphology and adaptive significance of antennular preening by the third maxillipeds. *Mar. Biol.* 40:261-276.
- Bauer, R.T. (1978) Antifouling adaptations of caridean shrimps: Cleaning of the antennal flagellum and general body grooming. *Mar. Biol.* 49:69-82.
- Bauer, R.T. (1979) Antifouling adaptations of marine shrimp (Decapoda: Caridea): Gill cleaning mechanisms and grooming of brooded embryos. *Zool. J. Linn. Soc.* 65:281-303.
- Bauer, R.T. (1981) Grooming behavior and morphology in the decapod Crustacea. *J. Crust. Biol.* 1:153-173.
- Bauer, R.T. (1989) Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic inference. In B.E. Felgenhauer, L. Watling, and A.B. Thistle (eds.): *Functional Morphology of Feeding and Grooming in Crustacea*. Crustacean Issues 6, Rotterdam: Balkema Press, pp. 49-73.
- Casanova, B., M. Brunet, and M. Segonzac (1993) L'impact d'une epibiose bacterienne sur la morphologie fonctionnelle de crevettes associees a l'hydrothermalisme medio-atlantique. *Cah. Biol. Mar.* 34:573-588.
- Chace, F.A., Jr. (1992) On the classification of the Caridea (Decapoda). *Crustaceana* 63:70-80.
- Christoffersen, M.L. (1986) Phylogenetic relationships between Ophroporidae, Atyidae, Pasiphaeidae, Alvinocarididae fam. n., Bresiliidae, Psalidopodidae and Disciadidae (Crustacea: Caridea: Atyoidea). *Bol. Zool., Univ. Sao Paulo* 10:273-281.
- Christoffersen, M.L. (1991) A new superfamily classification of the Caridea (Crustacea: Pleocyemata) based on phylogenetic pattern. *Zeitschr. Zool. Syst. Evol.* 28 (1990):94-106.
- Forest, J., and P. Cals (1977) Une deuxieme espece du genre *Bresilia* Calman, *B. corsicana* sp. nov. Comparison avec *B. atlantica* Calman (Crustacea Decapoda Bresiliidae). *Bull.n du Mus. Nat'l. d'Hist. Nat., ser. 3*, 453, *Zoologie* 316:549-565.
- Gebruk, A.V., N.V. Piménov, and A.S. Savvichev (1993) Feeding specializations of bresiliid shrimps in the TAG site hydrothermal community. *Mar. Ecol. Progr. Ser.* 98:247-253.
- Grassle, J.F. (1986) The ecology of deep sea hydrothermal vent communities. *Advances in Mar. Biol.* 23:301-362.
- Hessler, R.R., P. Lonsdale, and J. Hawkins (1988) Patterns on the ocean floor. *New Scientist.*, 24 March 1988, 1605:47-51.
- Hessler, R.R., and J.W. Martin (1989) *Austino-graea williamsi*, new genus, new species, a hydrothermal vent crab (Decapoda: Bythograeidae) from the Mariana Back-Arc Basin, western Pacific. *J. Crust. Biol.* 9:645-661.
- Holthuis, L.B. (1993) The Recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda), with an appendix on the order Amphionidacea. Leiden, The Netherlands: Nat'l. Natuurhist. Mus., 328 pp.
- Kuenzler, R.O., J.T. Kwasniewski, R.N. Jinks, R.C. Lakin, B.-A. Battelle, E.D. Herzog, L. Kass, G.H. Renninger, and S.C. Chamberlain (1997) Retinal anatomy

- of new bresiliid shrimp from the Lucky Strike and Broken Spur hydrothermal vent fields on the Mid-Atlantic Ridge. *J. Mar. Biol. Assoc. (U.K.)* (in press).
- Martin, J.W., and J.C. Christiansen (1995) A new species of the shrimp genus *Chorocaris* Martin and Hessler, 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge. *Proc. Biol. Soc. Wash.* 108:220-227.
- Martin, J.W., and R.R. Hessler (1990) *Chorocaris vandoverae*, a new genus and species of hydrothermal vent shrimp (Crustacea, Decapoda, Bresiliidae) from the western Pacific. *Contr. Sci., Nat. Hist. Mus. Los Angeles County* 417:1-11.
- Martin, J.W., J. Signorovitch, and H. Patel (1977) A new species of *Rimicaris* (Crustacea, Decapoda, Bresiliidae) from the Snake Pit hydrothermal vent field on the Mid-Atlantic Ridge. *Proc. Biol. Soc. Wash.* 00:000-000.
- Nation, J.L. (1983) A new method using hexamethyldisilazane for preparation of soft tissues for scanning electron microscopy. *Stain Tech.* 38:347-351.
- Nuckley, D.J., R.N. Jinks, B.-A. Battelle, E.D. Herzog, L. Kass, G.H. Renninger, and S.C. Chamberlain (1996) Retinal anatomy of a new species of bresiliid shrimp from a hydrothermal vent field on the mid-Atlantic Ridge. *Biol. Bull.* 190:98-110.
- O'Neill, P.J., R.N. Jinks, E.D. Herzog, B.-A. Battelle, L. Kass, G.H. Renninger, and S.C. Chamberlain (1995) The morphology of the dorsal eye of the hydrothermal vent shrimp, *Rimicaris exoculata*. *Vis. Neurosci.* 12: 861-875.
- Renninger, G.H., L. Kass, R.A. Gleeson, C.L. Van Dover, B.-A. Battelle, R.N. Jinks, E.D. Herzog, and S.C. Chamberlain (1995) Sulfide as a chemical stimulus for deep-sea hydrothermal vent shrimp. *Biol. Bull.* 189:79-76.
- Segonzac, M. (1992) The hydrothermal vent communities of the Snake Pit area (Mid Atlantic Ridge; 23° N, 3480 m). *Comptes Rd. Hebd. S. Acad. Sci., Paris* 314: 593-600.
- Segonzac, M., M. de Saint Laurent, and B. Casanova (1993) L'enigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale medio-atlantique. *Cah. Biol. Mar.* 34:535-571. [English trans., IFREMER, 1994. The enigma of the trophic behavior of alvinocaridid shrimps from the hydrothermal vent sites on the Mid-Atlantic Ridge, pp. 1-20]
- Tunncliffe, V. (1991) The biology of hydrothermal vents: Ecology and evolution. *Oceanogr. Mar. Biol. Ann. Rev.*, 1991, 29:319-407.
- Van Dover, C.L. (1995) Ecology of Mid-Atlantic Ridge hydrothermal vents. In L.M. Parson, C.L. Walker, and D.R. Dixon (eds.): *Hydrothermal Vents and Processes*. Geological Society Special Publication 87:257-294.
- Van Dover, C.L., B. Fry, J.F. Grassle, S. Humphris, and P.A. Rona (1988) Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge. *Mar. Biol.* 98:209-216.
- Van Dover, C.L., E.Z. Szuts, S.C. Chamberlain, and J.R. Cann (1989) A novel eye in "eyeless" shrimp from hydrothermal vents of the Mid-Atlantic Ridge. *Nature* 337:458-460.
- Wharton, D.N., R.N. Jinks, E.D. Herzog, B.-A. Battelle, L. Kass, G.H. Renninger, and S.C. Chamberlain (1997) Morphology of the eye of the hydrothermal vent shrimp, *Alvinocaris markensis*. *J. Mar. Biol. Assoc. U. K.* (in press).
- Wicksten, M.K. (1989) *Encantada spinoculata*, a new genus and species of shrimp from the Galapagos Islands (Caridea: Bresiliidae). *J. Crust. Biol.* 9:667-671.
- Williams, A.B. (1988) New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage. *Fish. Bull.* 86:263-287.
- Williams, A.B., and F.A. Chace, Jr. (1982) A new caridean shrimp of the family Bresiliidae from thermal vents of the Galapagos Rift. *J. Crust. Biol.* 2:136-147.
- Williams, A.B., and F.C. Dobbs (1995) A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii. *Proc. Biol. Soc. Wash.* 108:228-237.
- Williams, A.B., and P. Rona (1986) Two new caridean shrimps (Bresiliidae) from a hydrothermal vent on the Mid-Atlantic Ridge. *J. Crust. Biol.* 6:446-462.
- Wirsen, C.O., H.W. Jannasch, and S.J. Molyneux (1993) Chemosynthetic microbial activity at Mid-Atlantic Ridge hydrothermal vent sites. *J. Geophys. Res.* 98(B6): 9693-9703.