Antifouling Adaptations of Caridean Shrimps: Cleaning of the Antennal Flagellum and General Body Grooming

R.T. Bauer

Biological Sciences Department, California Polytechnic State University; San Luis Obispo, California, USA

Abstract

Structural specializations of chelipeds used by caridean shrimp in two kinds of grooming activity are described. In general body grooming, the chelipeds, and in some species, the last walking legs, nip, pick or brush material from the exoskeleton. When the cleaning chelipeds are the second pair, the carpal segment is multi-segmented, increasing distal flexibility which aids in grooming. Tufts of compound setae and setal "chela locks" are characteristic of cleaning chelae. In representatives from 13 of 15 caridean families surveyed, brushes of serrate setae surround the carpal-propodal joint of the first cheliped. This setal structure is used in the specific task of cleaning the chemotactile antennal flagellum. Cleaning brushes on the last walking legs of some species are involved in general body cleaning. Experiments on *Heptacarpus pictus* showed that when the cleaning chelipeds were ablated, body parts became fouled with epizoites and particulate debris in experimental shrimps, while control shrimps showed little fouling. Suggestions on the adaptive role of general body cleaning in these natant animals are discussed. A survey of cleaning characters in representatives from 15 caridean families suggest that such characters are rather constant within a family. A possible correlation between the taxonomic success of a family and the degree of development of general body cleaning is suggested.

Introduction

Caridean shrimps, important faunal components of many marine habitats, can be frequently observed cleaning the body with the third maxillipeds, chelipeds and last walking legs. The cleaning behavior of *Pandalus danae* has been described (Bauer, 1975), as has antennular cleaning (Bauer, 1977), gill cleaning and embryo care (Bauer, in press) in caridean shrimps. All studies have indicated that cleaning behavior prevents fouling of the body by epizooites and particulate debris. The present report continues my studies on caridean cleaning, and focuses on grooming done with the chelipeds and walking legs. Special attention is given to cleaning of the antennal flagellum and the general body surfaces. The purpose of this report is to describe the functional morphology of these cleaning behaviors and to report experiments on the adaptive value of general body grooming.

Materials and Methods

A list of the caridean species observed is presented in Table 1. General methods of observation have been given in Bauer (1977). The effects of ablating the cleaning chelipeds were observed in *Heptacarpus pictus*. Experimental shrimp had the second chelipeds removed, while controls had the first walking leg (never involved in grooming) ablated. Shrimps were placed in 4 to 5 l plastic buckets covered with many 2 to 3 mm holes through which seawater could circulate. These cages were hung in running unfiltered seawater. Attached to the cases, as settling plates for fouling organisms, were standard microscope slides and 50 x 70 mm rectangles of asbestos board. Experiments were conducted in 1974, from 8-25 February (25 shrimp in each treatment) and from July 22 - August 1 (20 shrimp, each treatment). Gravid females carrying early embryos were used to prevent interruption of the experi-

Table 1. Occurrence of antennal and general body cleaning behaviors in caridean species observed alive. X: Behavior observed; I: behavior inferred from morphology; -: behavior neither observed nor inferred

Species	Antennal cleaning with carpal-propodal brush of Cheliped I	General body cleaning by a pair of chelipeds	General body cleaning by last walking leg
Hippolytidae			
Heptacarpus pictus (Stimpson)	X	X	X
H. stylus (Stimpson)	X	X	X
H. paludicola (Holmes)	X	X	X
H. palpator (Owen)	I	I	I
H. taylori (Stimpson)	I	I	I
H. brevirostris (Dana)	X	X	I
Lysmata californica (Stimpson)	X	X	X
Pandalidae			
Pandalus danae	X	X	X
P. platyceros Brandt	X	I	I
P. hypsinotus Brandt	I	I	I
P. montagui tridens (Rathbun)	X	I	I
Pandalopsis dispar (Rathbun)	X	I	I
Crangonidae			
Crangon nigricauda (Stimpson)	X	X	-
Paracrangon echinata (Dana)	X	-	-
Alpheidae			
Alpheus sp. (San Diego)	-	X	X
Alpheus sp. (Gulf of California)	-	X	X
Betaeus macginitieae	-	X	X
B. harfordi Hart	-	I	I
Palaemonidae			
Palaemon ritteri	X	X	X

ment by molting — these individuals do not molt until after hatching of embryos (Bauer, 1976a). When, in periodic checks, hatching was observed in some females, the experiment was terminated. After preservation, various parts of the exoskeleton were examined by light microscopy for fouling.

A survey of the cleaning morphology of representatives from caridean families, based on behavioral observation, morphology of appendages and the literature, was conducted (Table 2). Those species in which only preserved material was examined were judged to possess a particular cleaning behavior if the appendage in question had the same structure or processes as homologous limbs used in cleaning by species observed behaviorally.

Results

Morphology of Cleaning Chelipeds

In caridean species observed preening the body, one of the two pairs of chelipeds characteristic of carideans was involved in grooming. Chelipeds used in preening are usually the more slender of the two pairs, bearing dense tufts of serrate or multiscaled setae on the chelae (Fig. 1). For example, in the hippolytids *Heptacarpus* spp. and *Lysmata californica,* the second chelipeds preen the body, while the first pair are heavier, used in macerating food. Similarly, in *Alpheus* spp. and *Betaeus* spp., the second chelipeds are for preening, while the first are much larger, functioning in agonistic behavior and prey capture. Moreover, the first pereiopods of *Crangon* spp. are subchelate, used in prey capture, while the second are slender preening chelipeds in *C. nigricauda.* In contrast, the first chelipeds of *Palaemon ritteri* are the grooming limbs, while the second pair are robust, used in agonistic behavior and food capture. In pandalids observed, the second chelipeds were used for grooming, but the first pair are small and slender, with vestigial chelae, used in food search (Bauer, 1975). In all species observed, preening was never the sole function of

cleaning chelipeds, which also functioned in food searching and handling.

In the hippolytids, alpheids, and pandalids studied, the cleaning (second) chelipeds possessed a multiarticulated carpal segment (Fig. 1). The carpus is subdivided into a variable number of segments which articulate with one another, increasing the flexibility of the limb. These chelipeds are amazingly mobile, with the carpus capable of being twisted into a variety of "s"-shaped and circular configurations during grooming. Subdivision of the second cheliped carpus is a character of taxonomic importance in the Caridea (Holthuis, 1955), being constant within each of the following families: Hippolytidae, Alpheidae, Pandalidae, Ogyrididae, Processidae, and Glyphocrangonidae. Subdivision of the carpus occurs only in the second chelipeds of carideans, not the first.

Palaemon ritteri is the only species observed in which the first chelipeds were used for grooming, and as indicated above, the carpus is entire. Wickler and Siebt (1970) reported that another caridean, *Hymenocera picta* (Gnathophyllidae), used its first chelipeds in grooming, and the first cheliped carpus is entire in this family. An atyid species, *Caridina nilotica,* uses both the first and second chelipeds in cleaning the body
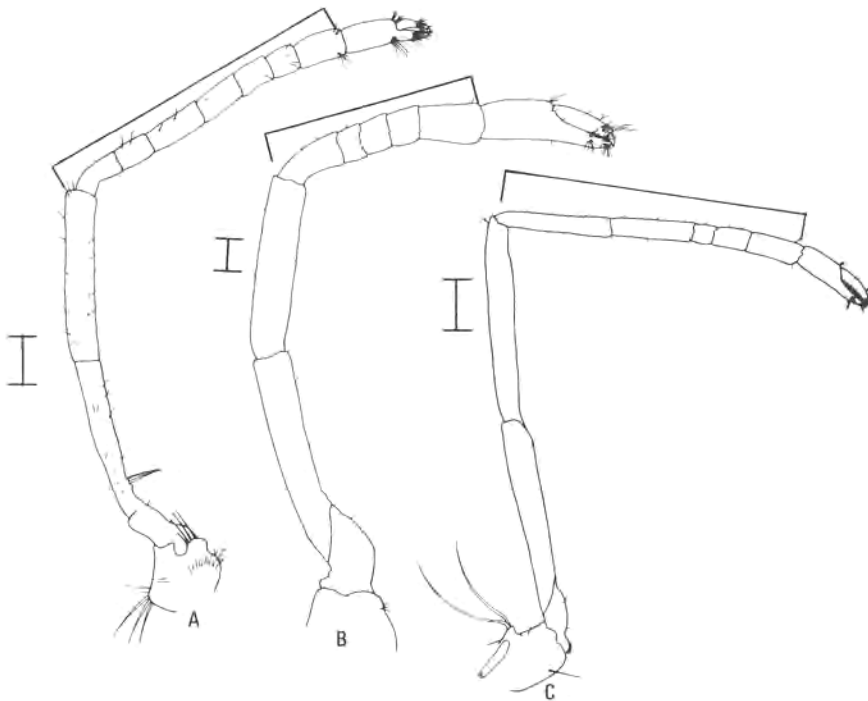

Fig. 1. (A) *Heptacarpus pictus;* (B) *Betaeus macginitieae;* (C) *Alpheus* sp. Cleaning chelipeds with a multisegmented carpus (bracketed). Scale bars = 1.0 mm

Table 2. Distribution of antennal and general body cleaning behaviors in representatives of caridean families. P: Present; A: absent. D: Direct behavioral observation; M: behavior inferred from limb morphology; L: from the literature

Family	Antennal grooming by carpal-propodal brush of Cheliped 1 (1)	General body grooming by chelipeds (2)	General body grooming by last walking leg (3)	Source of information
Hippolytidae				
Heptacarpus spp. Lysmata californica Hippolyte spp. Spirontocaris spp. Caridion gordoni (Bate)	P	P (Chelipeds 2)	P (but cleaning brush absent in Hippolyte californiensis)	1-3: D, M
Alpheidae				
Alpheus spp. Betaeus spp.	A (done by third maxillipeds)	P (Chelipeds 2)	P	1-3: D, M
Crangonidae				
Crangon spp. Paracrangon echinata	P	P or A (Chelipeds 2 in Crangon spp; these limbs absent in P. echinata)	P	1-3: D, M
Glyphocrangonidae				
Glyphocrangon spp.	P	P (Chelipeds 2)	A	1-3: M
Rhynchocinetidae				
Rhynchocinetes sp.	P	P(?) (Chelipeds 1 and/or 2)	A	1-3: M
Nematocarcinidae				
Nematocarcinus ensifer Smith		P (Chelipeds 1+2)	A	1-3: M
Oplophoridae				
Acanthephyra sp.	P	P(?) (Chelipeds 1+2)	P	1-3: M

(Fryer, 1960), and, in atyids, there is never carpal subdivision of chelipeds. From the information gathered here on carpal subdivision, two generalizations can reasonably be made: (1) when the carpus of the second cheliped is subdivided, that limb is a cleaning limb, (2) when the first chelipeds or first and second chelipeds are used in grooming, neither cheliped carpus will be subdivided.

It may be that when more than one pair of chelipeds are used in preening, there is no selective pressure for carpal subdivision, i.e., most areas can be groomed by one or the other pair of chelipeds. Cleaning by both pair of chelipeds in atyid shrimp has been reported above, and neither pair have subdivided segments. Similarly, the non-caridean shrimps Gennadas sp. (Penaeidea) and Stenopus sp. (Stenopodidea) groom with more than one pair (personal observation), and multiarticulation of cheliped segments is also lacking.

An exception to these generalizations has been found in Crangon nigricauda (Crangonidae) in which the second cheliped is used in grooming, but unlike other carideans using the same appendage, the carpus of the limb is not subdivided. In this species, a much greater mobility

Table 2 (continued)

Family	Antennal grooming by carpal-propoda brush of Cheliped 1 (1)	General body grooming by chelipeds (2)	General body grooming by last walking leg (3)	Source of information
Atyidae				
Caridina nilotica (Roux)	A	P	P	1: M; 2+3: M,L (Fryer, 1960)
Pandalidae				
Pandalus spp. *Pandalopsis* spp.	P	P	P	1-3: D, M
Stylodactylidae				
Stylodactylus sp.	P	A	A	1-3: M
Palaemonidae				
Palaemon spp. *Palaemonetes* spp. Palaemonid spp. Pontoniid spp.	P	P (Chelipeds 1)	P (in Palaemoniinae) A (in Pontoniinae)	1: D, M; 2: D,M,L (Schöne, 1961); 3: D,M,L (illustrations and species descriptions in Holthuis, 1951, 1952)
Gnathophyllidae				
Gnathophyllum americanum Guerin	P	P (Chelipeds 1)	A	1-3: M
Hymenocera elegans Heller *H. picta* Dana	P	P (Chelipeds 1)	A	1: M; 2: M, L (Wickler and Seibt, 1970); 3: M
Processidae				
Processa spp.	P	P (one or both Chelipeds 2)	A	1+3: M; 2: M, L (illustrations in Manning and Chace, 1971)
Procarididae				
Procaris hawaiana Holthuis	P	A (no chelipeds)	A	1-3: M
Pasiphaeidae				
Pasiphaea emarginata Rathbun	P	A	A (possibly by Pereiopod 4)	1-3: M

is found in the basal segments of the grooming chelipeds than in other carideans examined. Flexibility of the coxa-basal and basi-ischial joints, as well as that of the articulation of the coxa to the sternum, is much higher than in carideans such as *Heptacarpus* spp., *Pandalus* spp., *Palaemon* spp. and *Glyphocrangon* sp. examined. Apparently, the distal flexibility given by carpal subdivision to the second chelipeds of other species using them in grooming is replaced in *C. nigricauda* by basal flexibility. Otherwise, the second chelipeds of this species are like other grooming chelipeds, i.e., long and slender, with tufts of

compound setae at the tip (see Fig. 15 in Bauer, 1976b).

Table 2 summarizes the mode of cheliped grooming for representatives of 15 caridean families. In the Glyphocrangonidae and Processidae, the generalization that the second chelipeds are grooming limbs is made by inference from other families where the second cheliped carpus is subdivided and which have been observed in use as grooming limbs. In families such as the Pasiphaeidae, the doubt cast on cheliped cleaning was based on the observation that neither pair of chelipeds has a similar structure to known cleaning chelipeds, i.e.,

the limbs examined possessed a form appearing to be of little use in grooming of the kind described in the present study (see "General Body Grooming", below).

A common feature of caridean cleaning chelae is the presence of interdigitating stout setae (pegs, spines of other authors) on the tips of chelal fingers (chela lock; Bauer, 1975). Thompson (1965, 1966) has discussed the distribution of this character in caridean groups. Scanning electron microscopy has shown that a stout seta on the immovable (propodal) finger of the chela fits between two similar setae on the movable (dactylar) finger (Bauer, 1975; see Fig. 17 in Bauer, 1976b). Chela locks have been found in oplophorids, *Eugonatonotus* spp., hippolytids (Thompson, 1966) and pandalids (Chace and Manning, 1972). *Heptacarpus pictus* has chela locks on both pair of chelae (see Fig. 17 a-c in Bauer, 1976b). Chela locks may be a feature allowing the chelae to pick up and grasp small objects, which could be an important factor in the shrimp's ability to nip and pick at the exoskeleton during grooming. Exact opposition of cutting or crushing keels along the inner edges of the fingers may be effected by chela locks.

Other carideans appear to have similar adaptations for proper opposition of the fingers. In the *Rhynchocinetes* sp. examined, the tips of the fingers of both pair of chelae have several spinous setae which intermesh on closure of the chela. *Palaemon ritteri* has setae subequal in size and subterminal in position which appear to serve a similar function (see Fig. 17 in Bauer, 1976b).

Antennal Cleaning Brushes of the First Cheliped

Setal brushes on the first chelipeds of *Heptacarpus* spp., *Lysmata californica*, *Palaemon ritteri*, *Pandalus danae*, *Crangon nigricauda* and other carideans perform the very specific task of grooming the flagellum of the second antenna (Tables 1 and 2). Cleaning brushes used in antennal grooming were always located on either side of the carpal-propodal joint of Pereiopod 1 [Figs. 2, 3; and see Plate 3 in Bauer, 1975, and scanning electron microscope (SEM) Figs. 20, 21 in Bauer, 1976b]. The first cheliped may vary in size, structure and function in these different shrimps but, whatever these differences, the antennal cleaning brush is similar in form and location, with motor patterns involved in its use being alike. Sometimes, a group or row of serrate setae located distally on the carpus

simply arches over the carpal-propodal joint (*Procaris hawaiana*, *Crangon* spp.) These setae are in a "V"-shaped configuration in *Palaemon ritteri*, *Pandalus danae*, and *Heptacarpus pictus*. Propodal brushes are made of serrate setae set in rows parallel to the long axis of the segment and directed inferiorly. This brush is located on the medio-inferior side of the proximal end of the propodus. Setae in both carpal and propodal groups bear double rows of tooth setules, typical of setae involved in cleaning.

Morphological investigation of first chelipeds of shrimps not observed behaviorally revealed that in 13 of 15 families examined, antennal cleaning brushes are present and similar in form and location to those described above (Table 2). Only the Alpheidae and Atyidae lack these brushes, and the alpheids groom the antennal flagellum with a different appendage (see "Antennal Cleaning", below). Results of this survey indicate that presence or absence of an antennal cleaning brush on the first cheliped is a constant character within a caridean family.

Grooming Brush of the Last Walking Leg

Distal segments of the walking legs of shrimps examined are similar in shape and setation, except that there are setal brushes on the distal end of the propodal segment of the last leg in *Heptacarpus* spp., *Lysmata californica*, *Palaemon ritteri*, *Pandalus* spp., *Alpheus* spp., *Betaeus* spp. (but not *Crangon* spp.) This brush is composed of varying numbers of rows of serrate or multiscaled setae similar to setae on the third maxillipeds used in grooming (see Figs. 4 and 5 in Bauer 1977; Fig. 24 in Bauer, 1976b). *Pandalus danae* has three well developed brushes on the propodal segment, dorsolateral, ventrolateral and ventromedial in position (Plates 6-8 in Bauer, 1975).

In other carideans (Table 2), presence or absence of a propodal brush on the last leg seems to be a family characteristic (or at least characteristic for the majority of species within a family). For example, all hippolytids examined (except *Hippolyte californiensis*) have the brush. Within the Palaemonidae, all the Palaemoniinae (except *Leander* spp.) and Euryrhynchiinae have the brush, whereas the pontoniids do not (based on figures and species descriptions in Holthuis, 1951, 1952). *Crangon* spp. and *Paracrangon echinata* (Crangonidae) do not have this grooming brush, and examination of figures and species descriptions from many sources indicate its absence
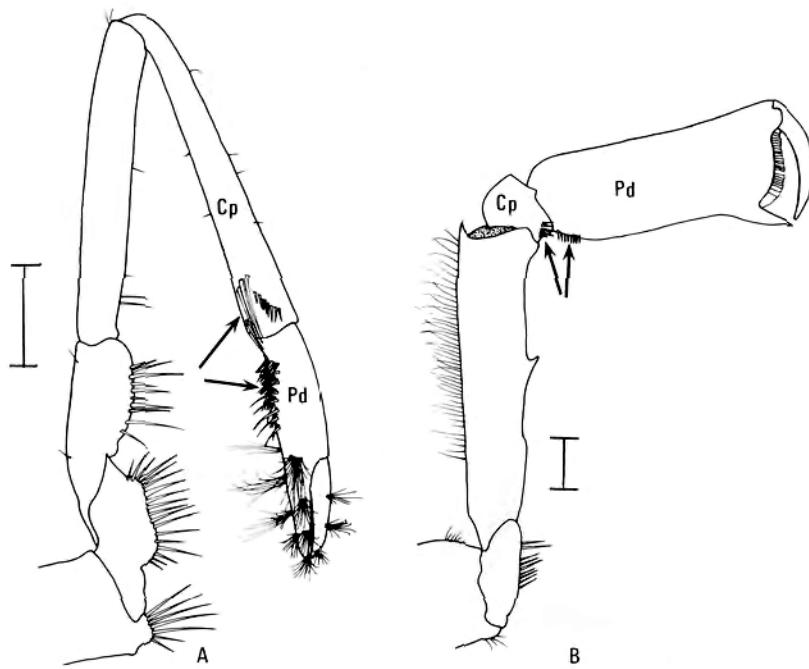
Fig. 2. (A) *Palaemon ritteri*; (B) *Crangon nigromaculata*. First chelipeds with carpal-propodal setal brushes (arrowed) used in cleaning antennal flagellum. Cp: carpus; Pd: propodus. Scale bars = 1.0 mm
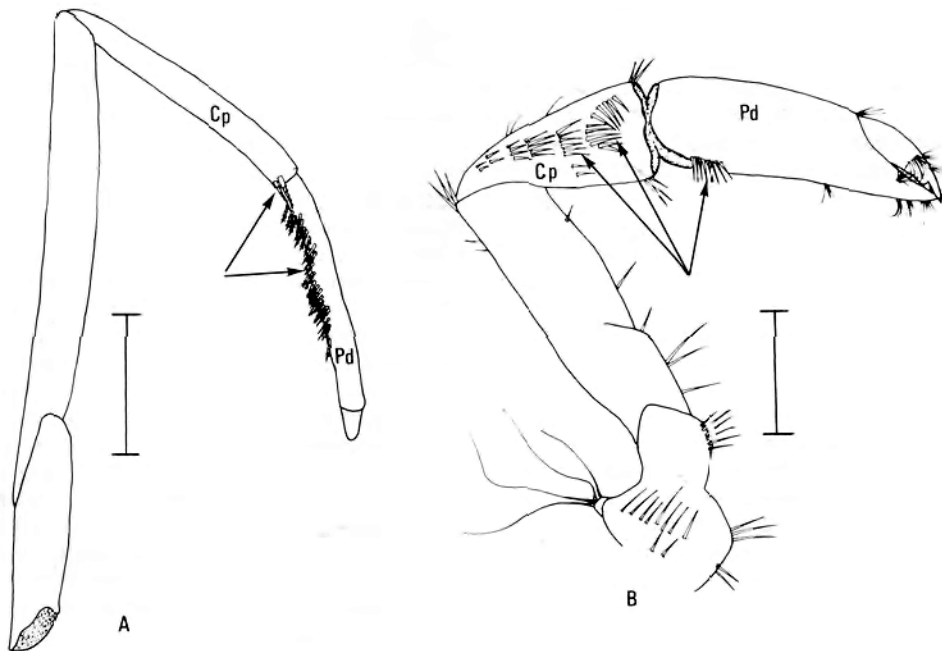

Fig. 3. (A) *Procaris hawiana*; (B) *Heptacarpus pictus*. First chelipeds with carpal-propodal brushes (arrowed). Cp: carpus; Pd: propodus. Scale bars = 1.0 mm
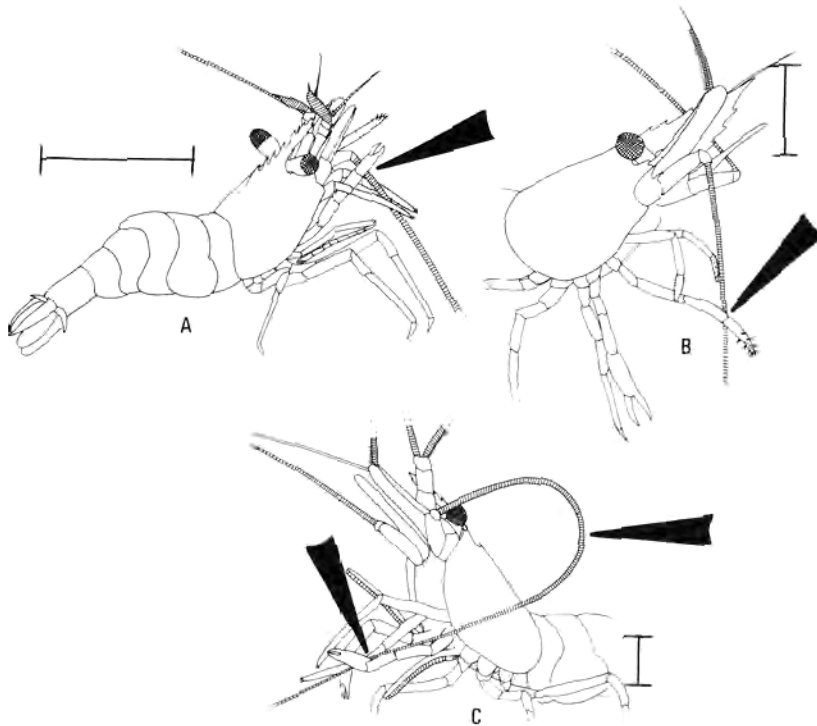
Fig. 4. (A) *Heptacarpus pictus*; (B) *Palaemon ritteri*; (C) *Lysmata californica*. Cleaning of antennal flagellum by the first cheliped (arrowed); see text for further explanation. Scale bars = 5.0 mm

in the related Glyphocrangonidae. Representatives of several families examined do not appear to possess this brush (Table 2).

Atyid shrimps are the only carideans examined in which the grooming brush of Pereiopod 5 is on the dactylar rather than propodal segment. In atyids, the flexor margin of the dactylus is bordered by stout serrate setae, with the setal comb being used for grooming in *Caridina* spp. (Fryer, 1960). Bouvier's figures in his 1925 monograph on atyids show the position of the dactylar comb to be constant within the family.

Antennal Cleaning

Rotation of the antennal flagellum forward is the first indication it will be cleaned. In all species observed, the carpal-propodal joint of the first cheliped flexes around the base of the flagellum (Fig. 4A), and is then depressed, sliding the setal brushes around the joint along the length of the flagellum (Fig. 4B), cleaning it. The characteristic loop formed in the flagellum as it is returned dorsally easily identifies this behavior (Fig. 4C). Occasionally, *Heptacarpus pictus*, *Palaemon ritteri* and *Pandalus danae* will clamp the third maxil-

lipeds around the flagellum when lowered and "scrub" it with rubbing movements. Although it would appear that more thorough cleaning could be done with the third maxillipeds, cleaning of the flagellum with the first cheliped is a quick, efficient movement.

The alpheid shrimps (*Alpheus* spp., *Betaeus* spp.) observed extensively groom the antennal flagellum not with the first chelipeds, but use the third maxillipeds only. Absence of the carpal-propodal brushes of the first chelipeds was noted earlier. The first chelipeds of these shrimps are large, strong and important in agonistic behavior (e.g. Nolan and Salmon, 1970; and own personal observation). These limbs appear to be too cumbersome to clean the antennal flagellae with their carpal-propodal joints, and the concomitant setal groups are absent (Fig. 5). A similar condition (third maxilliped grooming of antennal flagellae) has been observed in the atyid *Xiphocaris elongatus* (G. Fryer, personal communication).

General Body Grooming

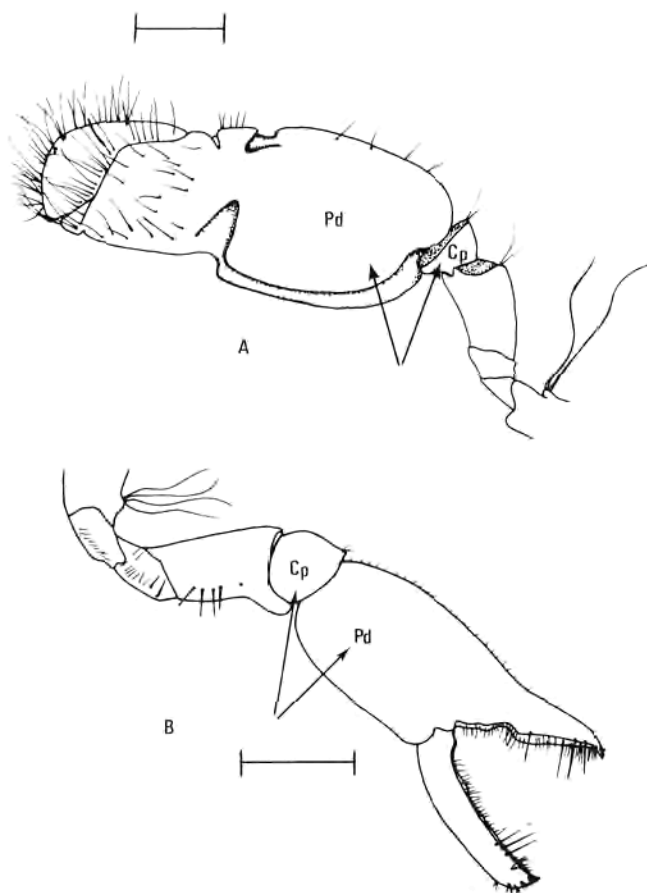General body grooming can be defined to include all preening activities exclusive of the following: brushing of re-

Fig. 5. (A) *Alpheus* sp; (B) *Betaeus macginitieae*. First chelipeds; arrows indicate locations where setal brushes used in antennal cleaning are found in other shrimps. Cp: carpus; Pd: propodus. Scale bars = 2.0 mm
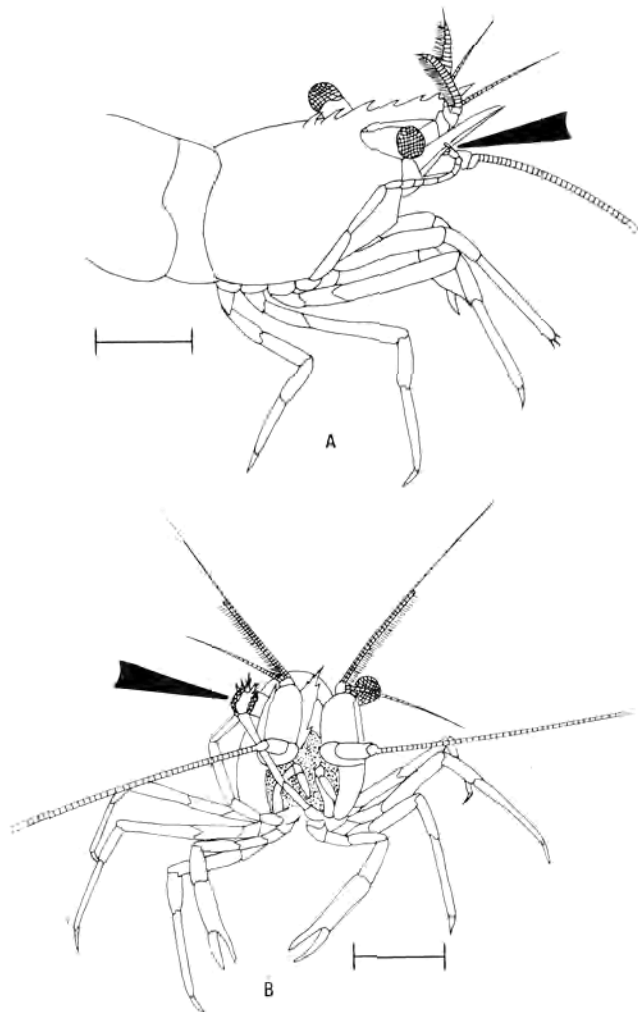

Fig. 6. (A) *Heptacarpus pictus*; (B) *Palaemon ritteri*. General body grooming; (A) second cheliped nipping at antennal scale (arrowed); (B) first chelipeds brushing the eye (arrowed). Scale bars = 2.0 mm

spiratory surfaces by the chelipeds; all cleaning by third maxillipeds and antennal flagellum cleaning by the first chelipeds. General body grooming encompasses all nipping and picking at body parts by the cleaning chelipeds and the brushing movements of the last walking legs.

Cleaning chelipeds and last walking legs share the task of general body cleaning. For example, in *Heptacarpus pictus* and *Palaemon ritteri*, the chelipeds clean most of the body, with the last legs making comparatively fewer and less complicated movements toward the abdomen and pleopods. On the other hand, the last legs of *Pandalus danae* play a much greater role in cleaning than in the above mentioned species (Bauer, 1975).

Cleaning movements of the chelipeds are similar in all species observed (Figs. 6, 7). Chelae move rapidly over the area being groomed, with picking, tugging and snapping by the chelal fin-

gers. The latter behavior occurs particularly if the region cleaned has an intricate topography. Cleaning chelipeds of *Heptacarpus picuts*, *Palaemon ritteri* and *Alpheus* spp. can clean all the cephaelothoracic area. Ventral abdominal areas, e.g. pleopods, abdominal pleurae etc., are preened by the chelipeds as well.

Certain postures of the body and cleaning limbs are characteristic of general body grooming. When some ventral area is being preened, the chelipeds reach back with a "U" shape (Fig. 7A). In *Heptacarpus pictus*, the abdomen is flexed beneath the body so that chelipeds can reach ventral abdominal areas. After cleaning of pleopods, the shrimp rids them of dislodged debris by fanning them. *Palaemon ritteri* is the most acrobat-
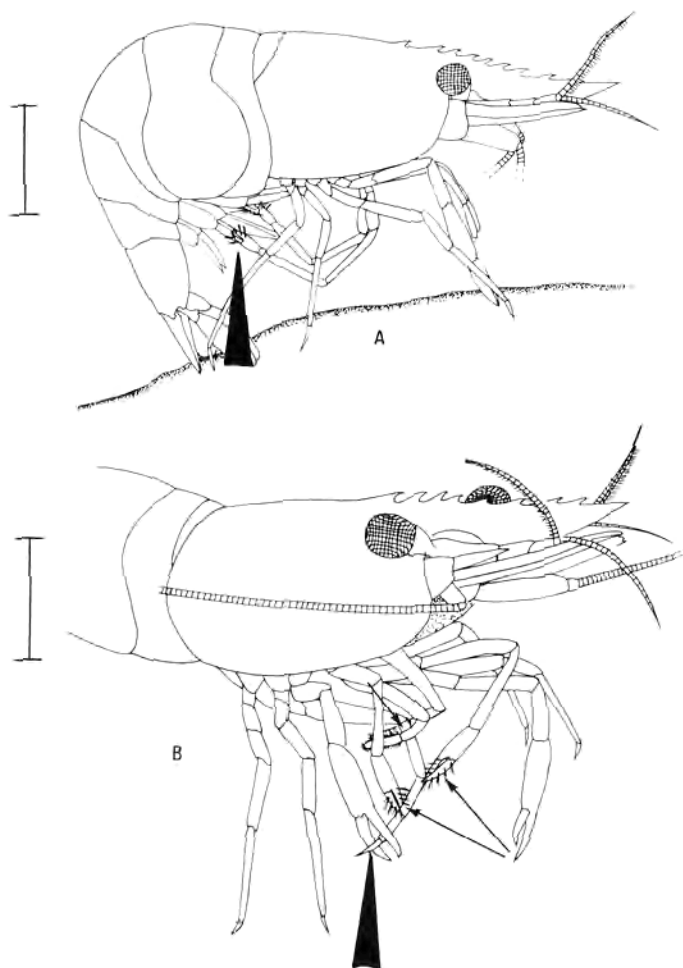
Fig. 7. *Palaemon ritteri*. General body grooming. (A) first chelipeds cleaning the pleopods (arrowed); (B) second cheliped holding a walking leg (arrowed) while leg is being cleaned by first chelipeds and third maxillipeds (light arrows). Scale bars = 5.0 mm
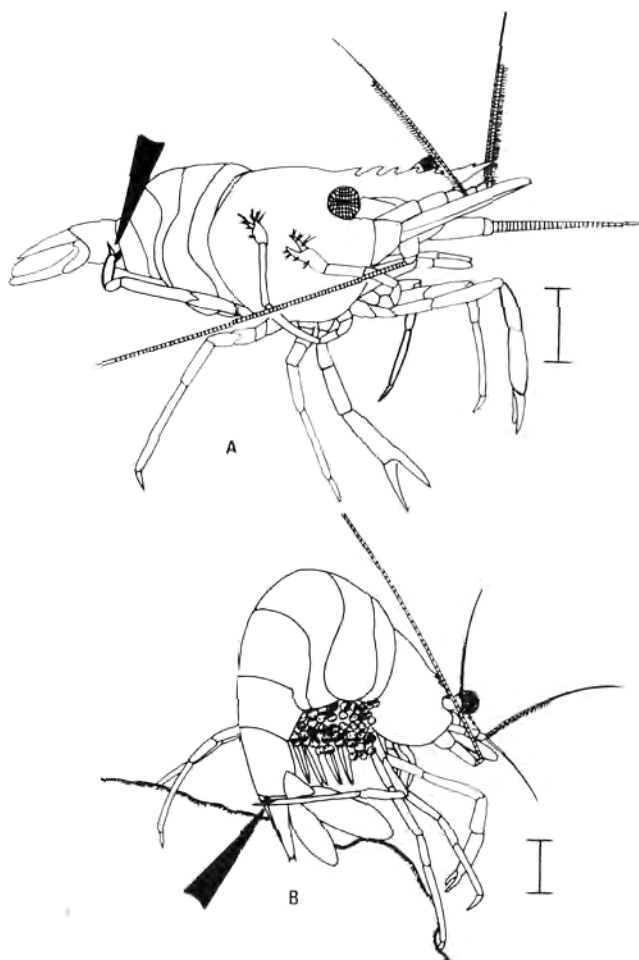
Fig. 8. *Palaemon ritteri*. General body grooming by setal brushes on last walking leg. (A) last abdominal segment being groomed (arrowed), note also grooming of carapace by the cleaning chelipeds; (B) tail fan being groomed (arrowed). Scale bars = 5.0 mm

ic of the shrimp observed in grooming. The body rests on the tip of the flexed tail posteriorly and on the tips of the extended legs anteriorly (Fig. 7A). *P. ritteri* also has the distinctive habit of holding one of the walking legs with the second cheliped while the cleaning chelipeds (and third maxilliped) groom the leg (Fig. 7B). *H. pictus*, when cleaning the tail fan, will hold its leading edge in place with the first chelipeds while preening the area with the cleaning chelipeds.

Grooming of the abdomen with the setal brush on the last walking leg involves a variety of scratching and rubbing movements (Fig. 8) which have been described in detail for *Pandalus danae* (Bauer, 1975).

Experimental Results

Cleaning chelipeds were removed from a group of *Heptacarpus pictus* (experimentals), as well as a control group (non-grooming leg ablated), with both groups being exposed to fouling in cages. After termination of the experiment, non-molted experimental shrimps qualitatively showed fouling of the exoskeleton; control shrimps did not. Macroscopically, most areas cleaned by the chelipeds, particularly setose areas, were fouled by particulate debris in experimentals. Smooth areas (e.g. the carapace) did not accumulate debris. The underside of the thorax, the bases of the legs, edge of the gill covers, and the pleopods had noticeable accumulation of material.
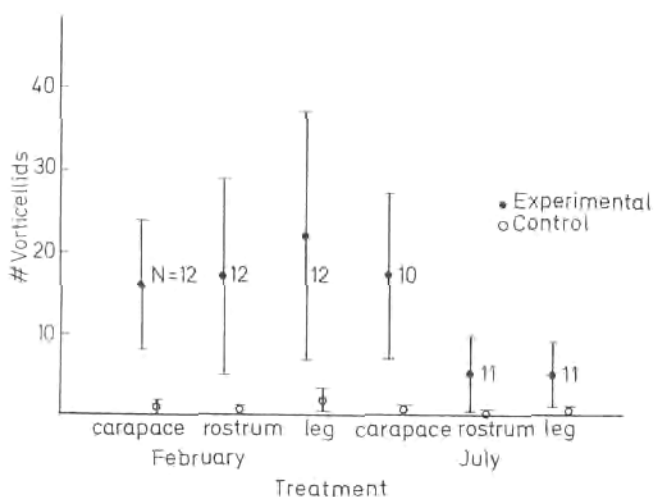
Fig. 9. *Heptacarpus pictus*. Fouling of body parts by vorticellid ciliates in control and experimental shrimps in ablation of cleaning cheliped experiments. $\bar{X}$, 95% confidence limits given

Microscopic examination of body parts showed that in experimentals a wide variety of micro-fouling organisms were attached. These organisms were much like those found on fouled antennules (Bauer, 1977), fouled gills and fouled embryos (Bauer, in press) in other experiments with *Heptacarpus pictus*. Much of the fouling was by *Leucothrix* sp., a long-chained bacterium widespread in marine habitats (Johnson *et al.*, 1971; Sieburth, 1975). Several kinds of diatoms, other algal cells, and stalked ciliates were attached to fouled areas. A hypotrichous ciliate was common in debris accumulations. A variety of coccoid and baciliform bacteria coated fouled regions (see Bauer, 1977, for SEM illustrations of fouling organisms).

To quantify epizoic settlement, an easily counted vorticellid ciliate was used as an indicator of fouling. Certain body parts normally cleaned by the chelipeds (Fig. 9) were removed from control and experimental shrimps, and vorticellid counts were taken. Since all shrimps were approximately the same size, simple counts, rather than vorticellid density, which would involve difficult measurements of exoskeleton area, were used. Fig. 9 gives the results from the two experiments, showing that in all cases experimental shrimps showed significantly higher fouling than controls.

Settling plates attached to the cages containing shrimps exhibited qualitatively similar fouling to that on the exo-skeleton of fouled shrimps, i.e., *Leucothrix* sp., other bacteria, diatoms, ciliates.

Discussion

Antennal Cleaning

Representatives of most caridean families groom the long antennal flagellum with carpal-propodal brushes on the first cheliped; in two families, the third maxillipeds were used. Antennal flagellae are long multisegmented structures waved about by the shrimp and are probably important sites of tactile and taste reception (Barber, 1961). Although no experimental work has been performed, fouling of non-groomed antennules of shrimp (Bauer, 1975; Bauer, 1977) indicates that frequent grooming of a sensory appendage prevents its fouling. It is probable that frequent cleaning of the antennal flagellum prevents fouling which might interfere with chemo- and mechanoreception.

In 13 of 15 families examined, a mechanism, the carpal-propodal brush of the first cheliped, has been developed to clean the antennal flagellum in a quick movement. Both the brush and the movement used are very similar to that used by ants in grooming their flagelliform antennae (Wilson, 1971). In ants, a curved brush on the fore tarsus of the first leg is used. As the foreleg and the antenna of ants are not homologous to the first cheliped and antennal flagellum (respectively) of shrimp, the foreleg brush and the behavior are clearly convergent to cheliped brushing of the antennal flagellum by shrimp. This convergence in insects may be indicative of high adaptive value in the structure and function of the carpal-propodal brush of Cheliped 1 in carideans.

General Body Grooming

Caridean shrimp engage in extended bouts of cleaning in which the preening chelipeds nip and pick at various parts of the cephalothorax, abdomen and appendages. Members of most caridean families appear to use one pair of chelipeds for general body grooming, but, in addition, some have a setal brush on the last walking leg which is also used in this behavior. In ablation experiments with *Heptacarpus pictus* in this report and *Pandalus danae* (Bauer, 1975), the areas normally groomed by cleaning limbs became fouled with microbial growth and particulate debris when not groomed. These experiments show that general body grooming prevents fouling of the exoskeleton by sediment, detritus and epizoic growth.

In a study on antennular preening in carideans (Bauer, 1977), the detrimental effects of fouling were strongly suggested by damage to olfactory setae on ungroomed antennules of Heptacarpus pictus. In the same species, individuals prevented by ablation from gill brushing suffered clogged and fouled gills which resulted, in some cases, in death (Bauer, in press); in the same study, embryos which were not cleaned by the female suffered heavy fouling and significant mortality. In the case of general body grooming, however, the deleterious effects of fouling, if any, are not so strongly suggested. For example, it is hard to see how the relatively light fouling of the carapace or abdominal pleurae could decrease a shrimp's chances of survival or reproductive success. Experiments designed with more extended fouling periods might elucidate this question. Although the frequent molting of caridean shrimp does remove all fouling, there might be periods in the life cycle of some species when molting rate is low enough to permit extensive fouling (e.g. when females are carrying embryos). Glynn (1970) has indicated that heavy algal fouling of sphaeromatid isopods may even inhibit molting.

The hard exoskeleton of shrimp (and all crustaceans) is periodically interrupted by areas of articulation, so that movement can take place between the segments and joints thus formed. Anything preventing movement between segments will interfere with locomotory and feeding movements of appendages and postural changes of the body. One function of general body cleaning may be to prevent fouling from building up on articular regions. Glynn (1970), considering experimentally fouled isopods, thought it likely that fouled individuals starved from epizoic interference with their feeding movements. It is also possible that a very heavy buildup of fouling organisms could prevent entry into narrow hiding places or interfere with locomotion simply by weighing the animal down.

In caridean shrimps, especially, fouling may interfere with swimming. The body design of carideans and other natantian decapods consists of a set of adaptations for swimming, particularly the backward swimming of the escape response. Partial streamlining seems to be accomplished by the subcylindrical and generally smooth cephalothorax. Flattened antennal scales serve as horizontal rudders for control during the escape response, while the long, laterally compressed rostrum acts as a stabilizing keel. Well developed abdominal musculature powers the backward swimming produced by the paddle-like tail fan. Epizoic fouling could reduce the efficiency and control of both this backward or rapid forward swimming by producing additional drag on the body and/or reducing mobility between body joints.

Additional indications that epizoic fouling is a selective pressure acting on swimming animals can be found by looking for presence or absence of anti-fouling mechanisms in other marine animals. Pickwell (1971) has remarked on the low incidence of fouling on the pelagic sea snake Pelamis platurus (L.). Heavy epizoic fouling only occasionally occurs on this reptile, and it is obviously incapable of the self-cleaning of limbed animals. Pickwell notes that the knotting of the body unique to P. platurus and its high frequency of molting, unparalleled for a snake, are mechanisms evolved, in part, in response to fouling pressure. Other sea snakes inhabit the bottom, and they do not exhibit these mechanisms, apparently because of their frequent contact with hard objects on the sea floor. By rubbing the body against hard substrates, prevention of fouling (and aid in skin shedding, the other function of knotting in P. platarus) can be achieved.

Scales of fish are protected by a secreted mucous which makes them generally unsuitable for attachment of invertebrate larvae. However, the barnacle Conchoderma virgatum can attach directly to fish in some cases (Beckett, 1968; Balakrishnan, 1969), although most individuals settle on ectoparasites (e.g. copepods) of the fish, rather than on their scales. Since the finned fishes have little ability to clean themselves, except for rubbing against some substrate, the task is performed in many cases by other fish or decapod cleaner shrimp, which feed on the ectoparasites or foulers. Thus, cleaning symbioses are important to marine fishes (Feder, 1966), while they seem to be absent from decapod shrimp, which can clean themselves.

Grooming behavior may have bestowed an adaptive advantage on the decapod (natantian) shrimps which might account, in part, for their extensive radiation (2000 species) relative to peracarid (mysid) shrimp (400 species) and euphausiid shrimp (100 species). The decapod caridoid shrimp occupy a much greater diversity of habitats and modes of life than these other malacostracan caridoid shrimps.

Within the Caridea, there may be a positive correlation between the number of pairs of general grooming limbs char-

acteristic of a family and its taxonomic diversity. Those families which have by far the greatest diversity in terms of numbers of genera and species, tend to have highly developed general body grooming, indicated by the presence of two pairs of general grooming limbs (chelipeds and last walking legs) (Pandalidae, Hippolytidae, Alpheidae, Palaemonidae: Palaemoninae, Atyidae). Results from this study have given no indication of general grooming specializations in the primitive family Procarididae, nor in the families Stylodactylidae and Pasiphaeidae — these families have few genera and species. An intermediate group, in which at least one pair of general cleaning limbs has been indicated in representatives studied, consists of the Crangonidae, Glyphocrangonidae, Oplophoridae, Rynchocinetidae, Nematocarcinidae, Gnathophyllidae, Processidae, and Palaemonidae: Pontoniinae.

In general, families which show the greatest diversification are active epibenthic forms abundant in nearshore marine, estuarine, and, in the case of atyids, freshwater environments where fouling pressures tend to be high. Groups in which general body cleaning is best developed may have been able to resist the deleterious effects of fouling, and have been free to diversify in these habitats.

Literature Cited

Balakrishnan, K.P.: Observations on the occurrence of *Conchoderma virgatum* (Spengler) (Cirripedia) on *Diodon hystrix* Linnaeus (Pisces). Crustaceana *16*, 101–103 (1969)

Barber, S.B.: Chemoreception and thermoreception. *In*: The physiology of Crustacea. Vol. II. Sense organs, integration, and behavior, pp 109–131. Ed. by T.E. Waterman. New York: Academic Press 1961

Bauer, R.T.: Grooming behaviour and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae). J. Linn. Soc. (Zool.) *56*, 45–71 (1975)

– Mating behavior and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). J. nat. Hist. *10*, 415–440 (1976a)

– Antifouling adaptations of caridean shrimp: grooming morphology and behavior, 289 pp. Ph.D. Dissertation, University of California at San Diego 1976b

– 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 (1977)

– Antifouling adaptations of marine shrimp: (Decapoda: Caridea): gill cleaning mechanisms and grooming of brooded embryos. J. Linn. Soc. (Zool.) (In press)

Beckett, H.S.: New record of the barnacle *Conchoderma virgatum* in the northwest Atlantic. J. Fish. Res. Bd Can. *25*, 2707–2710 (1968)

Bouvier, E.L.: Recherches sur la morphologie, les variations, et la distribution geographique des Crevetes de la familie des Atyides. Encycl. ent. (Ser. A) *4*, 1–370 (1925)

Chace, F.A. and R.B. Manning: Two new caridean shrimps, one representing a new family, from marine pools on Ascension Island (Crustacea: Decapoda: Natantia). Smithson. Contr. Zool. *131*, 1–18 (1972)

Feder, H.M.: Cleaning symbiosis in the marine environment. *In*: Symbiosis, Vol. 1. pp 327–380. Ed. by S.M. Henry. New York: Academic Press 1966

Fryer, G.: The feeding mechanism of some atyid prawns of the genus *Caridina*. Trans. R. Soc. Edinb. *64*, 217–244 (1960)

Glynn, P.W.: Growth of algal epiphytes on a tropical marine isopod. J. exp. mar. Biol. Ecol. *5*, 88–93 (1970)

Holthuis, L.B.: A general revision of the Palaemonidae (Crustacea: Decapoda: Natantia) of the Americas. I. The subfamily Euryrhynchiinae and Pontoniinae. Occ. Pap. Allan Hancock Fdn *11*, 1–332 (1951)

– A general revision of the Palaemonidae (Crustacea: Decapoda: Natantia) of the Americas. II. The subfamily Palaemoninae. Occ. Pap. Allan Hancock Fdn *12*, 1–396 (1952)

– The recent genera of the caridean and stenopodidean shrimps (class Crustacea, order Decapoda, super-section Natantia) with keys for their determination. Zool. Verh., Leiden *26*, 1–157 (1955)

Johnson, P.N., J. McN. Seiburth, A. Sastry, C.R. Arnold and M.S. Doty: *Leucothrix mucor* infestation of benthic Crustacea, fish eggs, and tropical algae. Limnol. Oceanogr. *16*, 962–969 (1971)

Manning, R.B. and F.A. Chace, Jr.: Shrimps of the family Processidae from the northwestern Atlantic Ocean (Crustacea: Decapoda: Caridea). Smithson. Contr. Zool. *89*, 1–41 (1971)

Nolan, B.A. and M. Salmon: The behavior and ecology of snapping shrimp (Crustacea: *Alpheus heterochelis* and *Alpheus normani*). Forma Functio *4*, 289–335 (1970)

Pickwell, G.V.: Knotting and coiling behavior in the pelagic sea snake *Pelamis platurus* (L.). Copeia *71*, 348–350 (1971)

Schöne, H.: Complex behavior. *In*: The physiology of Crustacea, Vol. II. pp 465-520. Ed. by T.H. Waterman. New York: Academic Press 1961

Sieburth, J. McN.: Microbial seascapes, 200 pp. Baltimore: University Park Press 1975

Thompson, J.R.: Comment on phylogeny of section Caridea (Decapoda: Natantia) and the phylogenetic importance of the Oplophoroidea. Proc. Symp. Crustacea (Mar. biol. Ass. India) *1*, 314-326 (1965)

– The caridean family Bresiliidae (Decapoda: Natantia). A revision and a discussion of its validity and affinities. Crustaceana *11*, 129-140 (1966)

Wickler, W. und U. Seibt: Das Verhalten von *Hymenocera picta* Dana, einer Seesterne fressenden Garnele (Decapoda: Natantia: Gnathophyllidae). Z. Tierpsychol. *27*, 352-368 (1970)

Wilson, E.O.: The insect societies, 548 pp. Cambridge: Belknap Press 1971

Raymond T. Bauer
Biological Sciences Department
California Polytechnic State University
San Luis Obispo, California 93407
USA