

# Grooming behavior and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae)

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*Accepted for publication July 1974*

Grooming or cleaning is a frequent behavioral activity of the shrimp *Pandalus danae*. Setal brushes on thoracic limbs scrape and rub other appendages and general surfaces of the exoskeleton. Chelate limbs nip and pick at edges of crevices in the cephalothoracic region. Scanning electron microscopy reveals that the setae composing the grooming brushes are equipped with characteristic tooth- and scale-like setules which serve as the actual rasping devices. Antennules, antennae and pereopods are frequently preened by the third maxillipeds and first pereopods, while large areas of the exoskeleton are cleaned by the third pair of walking legs and the chelate limbs.

Shrimp with the general cleaning limbs ablated develop significantly greater infestations of the epizoic suctionary *Ephelota* than animals allowed to groom. Olfactory hairs on the antennules of shrimp deprived of the third maxillipeds become fouled with diatoms and debris while those on controls do not. Grooming behavior clearly prevents a build-up of settling organisms between molts and repeated cleaning of sensory sites is essential in maintaining contact with the environment.

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## INTRODUCTION

A characteristic of the marine environment is the abundance of the larvae and spores of sessile organisms and the limited amount of suitable surface for

their attachment. Clean surfaces placed in marine waters invariably become covered in time with sedentary animals and benthic plants. Hard surfaced marine animals (bryozoans, molluscs, echinoderms, crustaceans) and benthic algae are utilized as substrates by bacteria, diatoms, sessile protozoans, hydroids, bryozoans, tubicolous polychaetes, barnacles and algae. These organisms can be deleterious to their hosts. Overgrowth of sensory and respiratory surfaces or openings, interference with locomotion, injury to host tissues with subsequent infection are types of damage epizoites might inflict on their animal substrates.

Another feature of the aquatic environment is that wind, waves, currents, river runoff and the activities of living organisms put sediment and detritus into suspension in the water column. Such materials can clog openings and cover surfaces through which contact between the internal environment of the animal and the external environment must take place, e.g., gill membranes, chemoreceptor sites. Sediment and detritus can interfere with feeding and locomotory activities if not removed in some manner.

Since marine animals face the danger of being overgrown by epizoites and/or smothered by particulate matter in the water, defenses against being fouled have been developed. Among the solutions to the problem of "keeping clean" is the removal of foreign particles, epizoites and ectoparasites by appendages and processes of the animals themselves. The pedicellariae of echinoderms, the avicularia and vibracula of ectoprocts are commonly assumed to discourage small predators and the larvae of settling animals (Ryland, 1970). The seta of a bryozoan vibraculum is swept over the colony, dislodging sediment which may smother it (Ryland, 1970). Sediment settling on the surfaces of many marine animals is entangled in mucus which is carried off the animal by ciliary currents, e.g., corals and anemones (Hyman, 1940: 613), asteroids (Hyman, 1955: 374).

Scattered reports in the literature indicate that caridean shrimp spend a large proportion of time and energy in grooming (cleaning, preening). Doflein (1910) has briefly described cleaning of the exoskeleton and brushing of the gills by the setose first chelae of *Palaemon xiphias* Risso. Höglund (1943) reported that cleaning is a process recurring daily in *Palaemon squilla* (L.), and remarked upon its importance prior to spawning. Preening with the chelate limbs has been observed in two species of *Alpheus* (Nolan & Salmon, 1970) and in the gnathophyllid shrimp *Hymenocera picta* Dana (Wickler & Seibt, 1970). The atyid shrimp *Caridina* cleans its pleopods with the chelipeds and scrapes abdominal surfaces with a row of stout setae ("spinules") on the dactyl of the last walking leg (Fryer, 1960). Needler (1931) stated that *Pandalus danae* cleans the pleopods thoroughly before egg-laying, although she did not indicate the appendages used.

Time- and energy-consuming activities can be assumed, *a priori*, to be important elements of an animal's adaptational repertoire. Grooming is such an activity in the life of caridean shrimps, but has not been analyzed in detail. Grooming is defined as the scraping and brushing of appendages and general body surfaces by specialized setal groups on certain thoracic legs. Nipping and picking at the exoskeleton by the chelate appendages is also a part of preening. Cleaning movements of the shrimp *Pandalus danae* and the structures it uses to carry them out are described in this report, and hypotheses on the adaptive value of grooming have been tested by some field experiments.

## MATERIALS AND METHODS

*Pandalus danae*, the "coonstripe" or "dock" shrimp, occurs along the eastern Pacific coast from Sitka, Alaska (Rathbun, 1904), south to San Luis Obispo Bay, California, at a depth of 18-180 m (Goodwin, 1952), usually on sand or gravel bottoms (Butler, 1964), but also on docks and pier pilings. This species is protandric (Berkeley, 1930).

Animals used in this study were collected at night by dip-netting through algae growing along the floating docks at the University of Washington's Friday Harbor Laboratories in May and June 1973. Most direct observations were made on animals kept in laboratory water tables with running seawater, but some were made on animals on the floating docks and pier pilings utilizing scuba. Analyses of movements were made from still photographs of animals in aquaria taken with a 35 mm reflex camera and electronic flash of 1/1500 second duration. Setal structure was examined by light and scanning electron microscopy (SEM). Specimens were preserved in formalin, desiccated in a freon critical point dryer and vacuum coated with a 150-200 Å thickness of gold-palladium for observation with a Cambridge S-4 SEM.

## MORPHOLOGY AND BEHAVIOR

All external surfaces of the shrimp are groomed by setal groups on the third maxillipeds, first and fifth pereopods, and by the chelae of the second pereopods. Grooming structures have been identified by their morphology and by observations on their use. Each thoracic appendage with a grooming structure primarily cleans a specific section of the animal's body (Fig. 1), although there are areas of overlap. Preening is never the sole activity of these limbs—they also function as locomotory, feeding and sensory appendages.

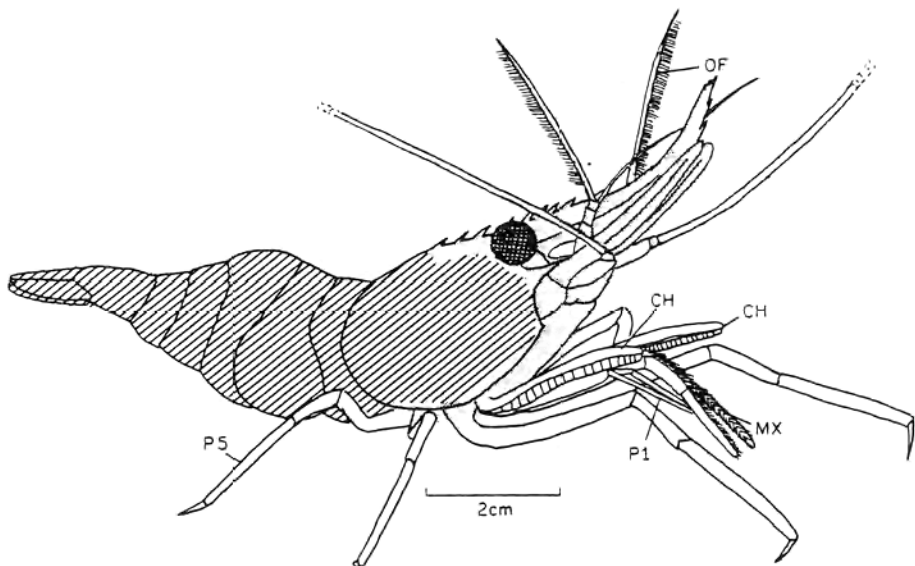


Figure 1. Map of *Pandalus danae* showing regions groomed by different cleaning limbs. Hatched areas are cleaned by pereopods 5 (last walking legs); stippled areas by pereopods 2 (chelipeds); unmarked areas by the third maxillipeds; CH, chelipeds; MX, third maxillipeds; OF, outer flagellum of antennule; P1, P5, pereopods 1, 5.

*Third maxillipeds*

The third maxillipeds are large pediform appendages which assist in food handling and which are important preening limbs. As in most carideans, the number of segments in this limb has been reduced from seven to four (Fig. 2).<sup>\*</sup> Dense setation on the medial surface of the carpus and propodus-dactylus is characteristic of the appendage, with relatively few setal groups on the lateral sides. Large compound setae with complex setulation are arranged in closely spaced dorsoventrally oriented rows. The structure and placement of these setae show that they are grooming devices, used by the animal as rasps to scrape and clean certain parts of the body.

Stout serrate setae with tooth- or blade-shaped setules comprise most of the grooming setae on the propodus-dactylus (Plate 1A, B, C), and are also the dorsal-most setae in the carpal rows. They are naked along the proximal third to half of the setal shaft, with two types of setules distally. On one side of the seta, there is a double row of broadly-based tooth setules which curve slightly toward those of the opposite side and also toward the tip of the seta. These setules attain maximum size in the middle of the compound area and at the tip of the shaft lie almost parallel to it (Plate 1B). Scale-like setules are situated on the other side of the seta, arising from a narrow raised area on the setal shaft (Plate 1D). Scale setules are arranged in wing-like pairs, a scale of a pair often slightly offset from its partner. Each scale is incised around its border to form several finger-like subsetules. These setules are slightly raised above the surface of the shaft and the subdivided edges are oriented towards the tip of the seta. Scales terminate subapically, and the last few are not free of the setal surface, appearing only as raised areas of the same contour. Thomas (1970) has described similar setules with light microscopy from thoracic coxal setae (setobranchs) of the crayfish *Austropotamobius pallipes* (Lereboullet). Setae of this morphology are found on the third maxillipeds and in the setal brushes of the last walking legs, which are also used to groom areas of the exoskeleton.

Most setae in the carpal rows lack tooth setules. Setules of these setae resemble scale setules in being subsetulate; however, they are longer, narrower, and many of them seem to arise from definite sockets (Plate 2A, B). Setulation is again restricted to the distal two-thirds or half of these setae, and the same kind of setule is found surrounding the setal shaft. Setules on opposite sides of the shaft do differ in their orientation to the seta. A double row of setules on one side is almost at right angles to the shaft (except near the tip), while those surrounding the rest of the seta are parallel to it and pointing towards the tip (Plate 2C, D). The latter are all elevated above the setal surface. Setae of this type are also found in the first several rows of the propodus-dactylus, but are surrounded both dorsally and ventrally by the serrate setae described above.

In the rows on the limb, setae are elevated above the appendage surface at an angle of approximately 45° with all setae pointing distally—setae in the dorsal portion of the rows are directed dorso-distally, those in the ventral part ventro-distally. An exception are some serrate setae on the dorsal edge of the

<sup>\*</sup> Balss (1940-61: 141) gives the homologies of the four segments: coxa, basis + ischium + merus, carpus, and propodus + dactylus; although Calman (1909: 269) believes the first segment is the coalesced coxa and basis. Berkeley's (1928) work on the musculature of *Pandalus danae* supports the former scheme.



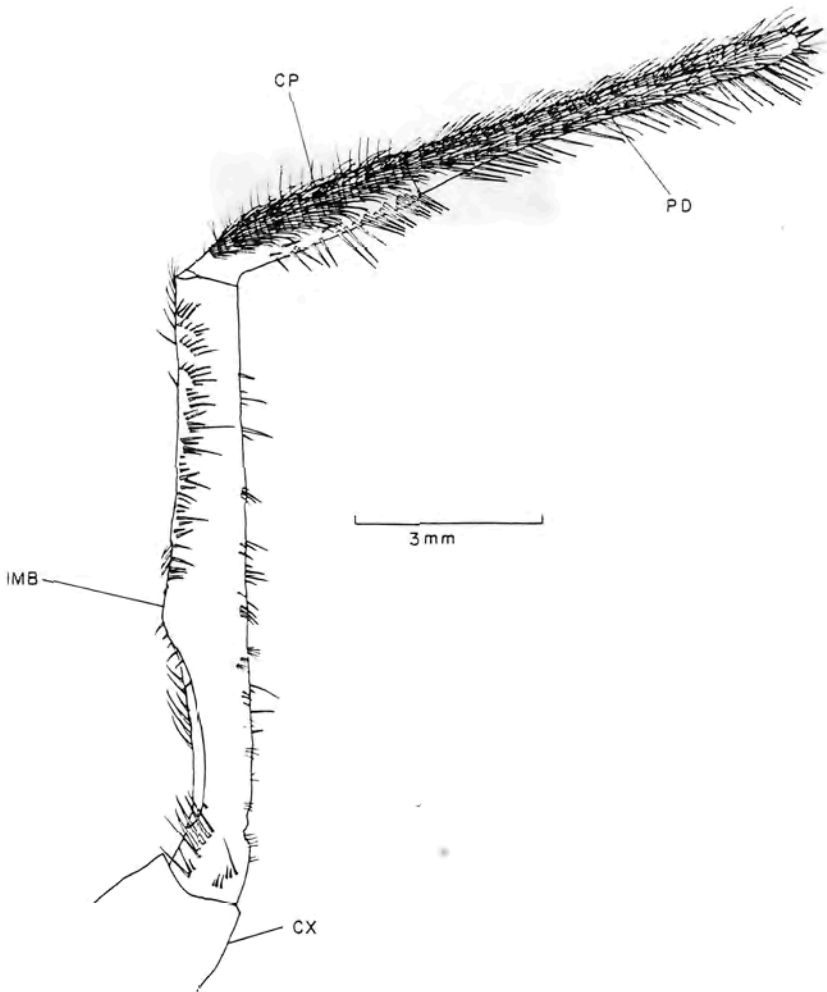


Figure 2. Left third maxilliped, medial view: CP, carpus; CX, coxa; IMB, fused basis, ischium, merus; PD, propodus-dactylus.

carpal rows, which rise straight off the segment. Tooth setules of serrate setae and the double rows of carpal setae face toward the surface of the limb. All the grooming setae articulate with the limb in a deep socket, allowing considerable freedom of movement.

When the shrimp is at rest, the third maxillipeds are held out in front of the animal (Fig. 1). Flexibility between carpus and propodus-dactylus is slight, so that the two segments function together as one rod-like unit. Assistance in seizing larger morsels of food and especially in pinning such items against the substratum with the heavy claw-like setae at the tip of the limb are functions of the third maxillipeds. Grooming acts, however, are the most frequent movements made by these appendages. The third maxillipeds clean the antennular flagella, the pereopods, and, together with the first pereopod, the antennal flagella.

The antennules of *Pandalus* show typical decapod structure, with an inner whip-like flagellum and a stouter outer flagellum bearing the rows of

thin-walled aesthetascs (Figs 1 and 3). Behavioral, ultrastructural and electrophysiological studies of these delicate setae indicate that they are a site of distance chemoreception in decapod crustaceans (Laverack, 1968). Outer flagella are usually held upright and rotated about the distal segment of the antennular peduncles so that the rows of aesthetascs are directed out laterally. Apparently arrhythmic twitching or flicking of the outer flagella is typical, probably to increase circulation of water about the sensory setae. Inner flagella point antero-laterally on either side of the rostrum.

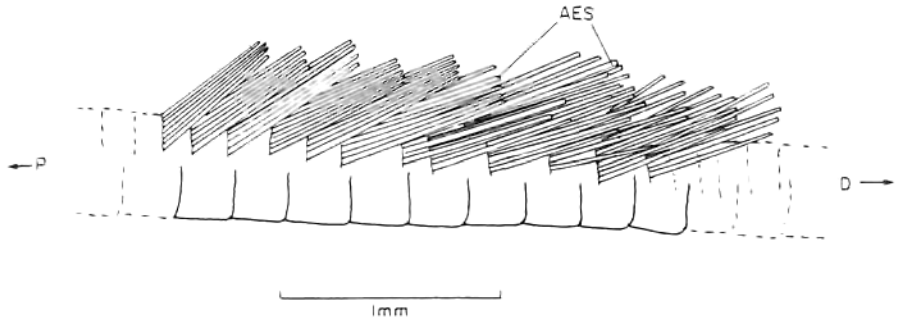


Figure 3. Portions of the outer flagellum of the left antennule: AES, aesthetasc; D, distal; P, proximal.

An act of antennular wiping involves only one antennule of the pair and contains the following sequence of events: the outer flagellum is rotated on the peduncle so that the aesthetasc rows face forward; simultaneously, the broad antennal scale of the same side is spread outwards to allow passage of the inner and outer flagella, which are flexed ventrally; the inner flagellum leads the way followed by the outer, with the aesthetascs in the median sagittal plane; at the same time, the third maxillipeds spread apart and are raised upwards to close on the bases of the flagella; the movements of the flagella are reversed while the third maxillipeds are depressed so that the inner and outer flagella and aesthetascs are pulled through and scraped by the setae of the carpus described above (Fig. 4A-C). At the end of the act the antennule is held up in its former position while the third maxillipeds autogroom—a process described below. A bout of antennular cleaning may be composed of one to several acts; antennules can be groomed alternately, or one of the pair may be groomed successively. Bouts of antennular cleaning can be intermixed with antennal and pereopod preening. Experimental evidence given in a later section shows that this grooming keeps the antennular flagella free of fouling particles and epizotes, particularly benthic diatoms. An efficient rasping surface for this function is formed by the complex setulation of the carpal setae, with the vast array of serrate projections on the setules.

The reduced first legs, the chelate limbs, and the three pairs of walking legs (pereopods 3, 4, 5) are cleaned by the third maxillipeds (mainly by the propodus-dactylus). Wiping of the walking legs, in particular, is a frequent behavior. Lateral movement of the third maxillipeds occurs as the walking leg is swung forward; one of the third maxillipeds slips up and over the leg so that it is grasped between the two grooming surfaces; the leg is drawn back through the appressed limbs which swing back medially into their original position (Fig.

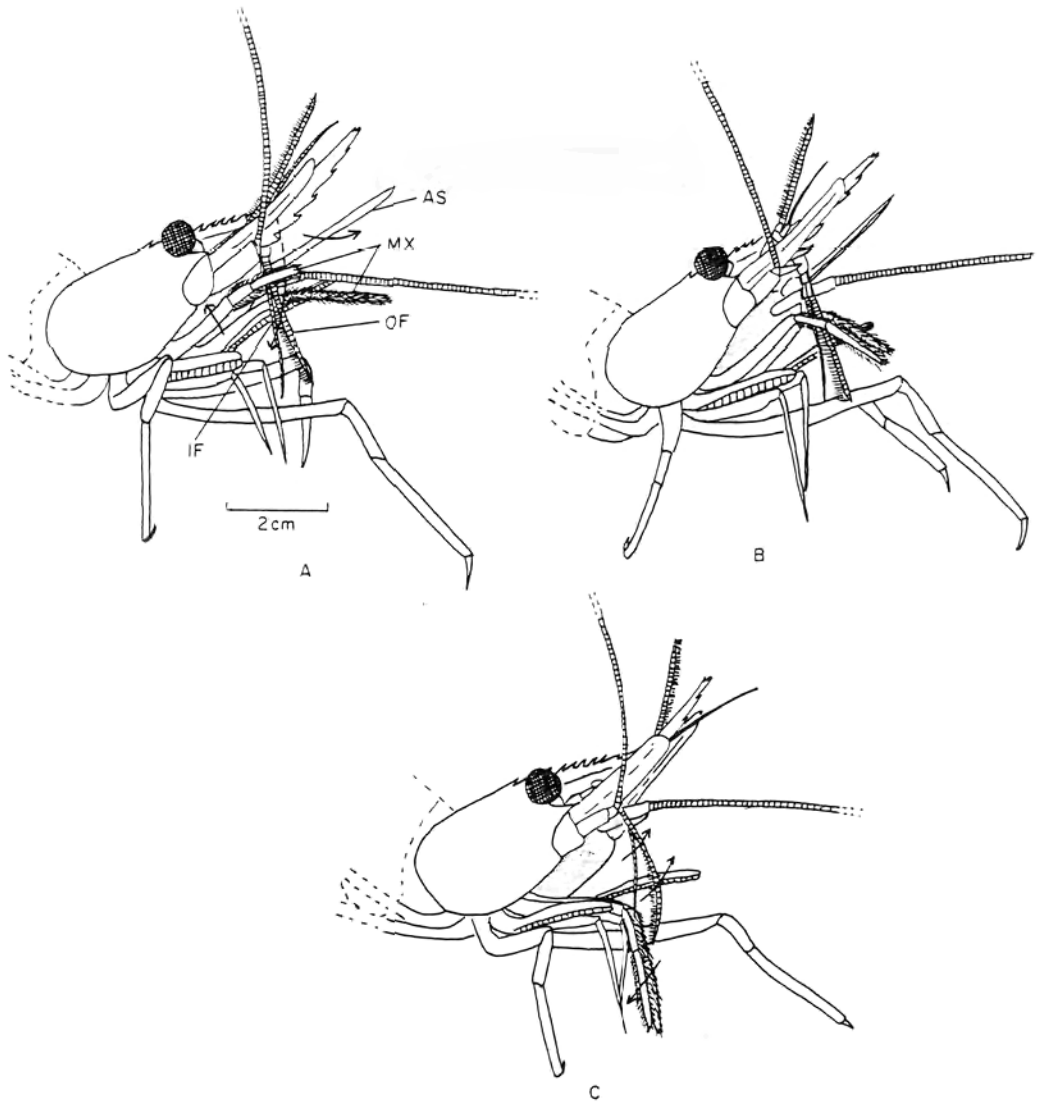


Figure 4. Antennular grooming: A, left antennule depressed, third maxillipeds reaching up; B, third maxillipeds beginning to scrape left antennular flagellum; C, right antennule returning to upright position: AS, antennal scale, IF, OF, inner and outer flagellum of antennule; MX, third maxilliped.

5A, B). To reach back to posterior legs or to the bases of the legs, the two grooming segments are flexed on the preceding segment (Fig. 5C); the segments are extended as the leg is drawn back. The last walking leg reaches under the first and second legs, the second under the first to get into position to be cleaned. Preening bouts vary from one to several acts, with one or more legs cleaned successively or in different combinations. Walking legs are in constant contact with the substratum and often become noticeably fouled with sediment and debris, especially the tips. Extraneous material is stripped off the legs by cleaning, clearly showing its effectiveness. Setae on the propodus-dactylus, with the stout tooth setules, seem better adapted to scraping the hard

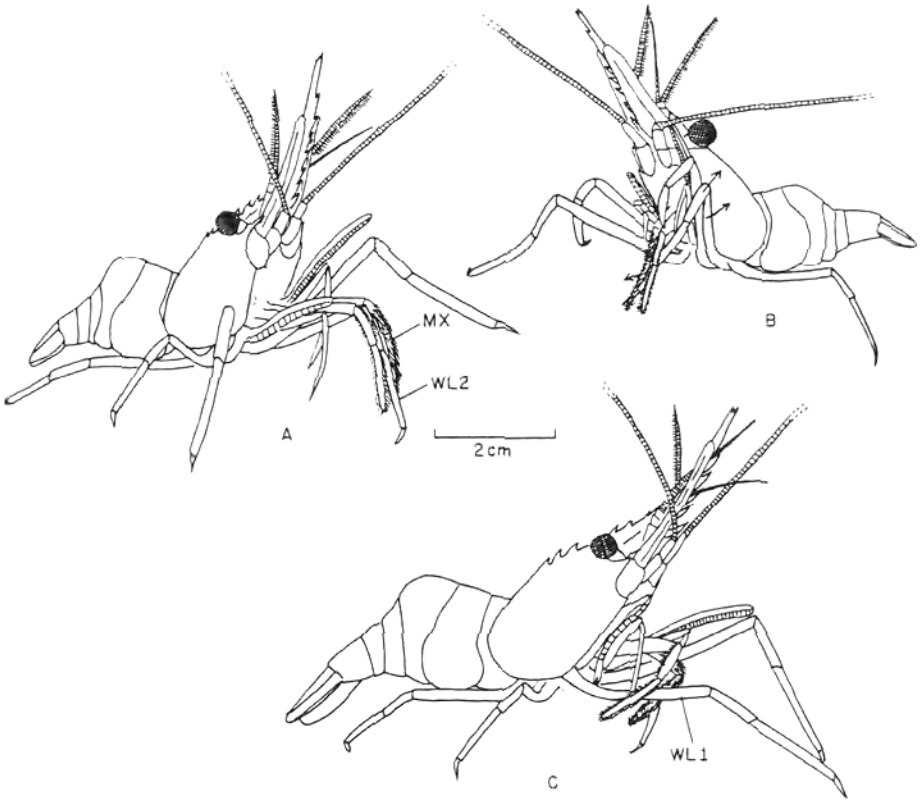


Figure 5. Leg grooming: A, third maxillipeds grasping left second walking leg; B, leg being pulled through grooming setae; C, maxillipeds reaching to base of first walking leg; MX, third maxilliped; WL 1, 2, walking legs 1, 2.

surfaces of the pereopods than do the carpal setae, whose finer setulation is better suited to groom the delicate olfactory hairs of the antennule.

The folded second pereopods (Fig. 1) move medially to be grasped and scraped by the third maxillipeds. Pereopods 1 are always in close proximity to the third maxillipeds. A first pereopod reaches between the third maxillipeds to be cleaned by scrubbing movements, the only such behavior by the third maxillipeds except for autogrooming. Perhaps cleaning of pereopod 1 and autogrooming are combined.

Fouling of the third maxillipeds with the material they scrape off the antennules and pereopods would soon occur if they were themselves not cleaned. Fouling is prevented by autogrooming. After each grooming act, the third maxillipeds rub back and forth against one another, few to several times (Fig. 6A-E). As one member of the pair moves down, the other is lifted up in the opposite direction. Setae of the ventrally moving limb comb and sweep through the grooming setae of the opposite side; when the movements are reversed, the cleaning action is reciprocated. If a large piece of debris or sediment is caught on the setae, these movements transfer it back and forth between the two sides but always further toward the tip of the limb; after a few autogrooming acts, a macroscopic bit of debris can be seen moving down to the tip of the third maxillipeds where it drops off. After antennular

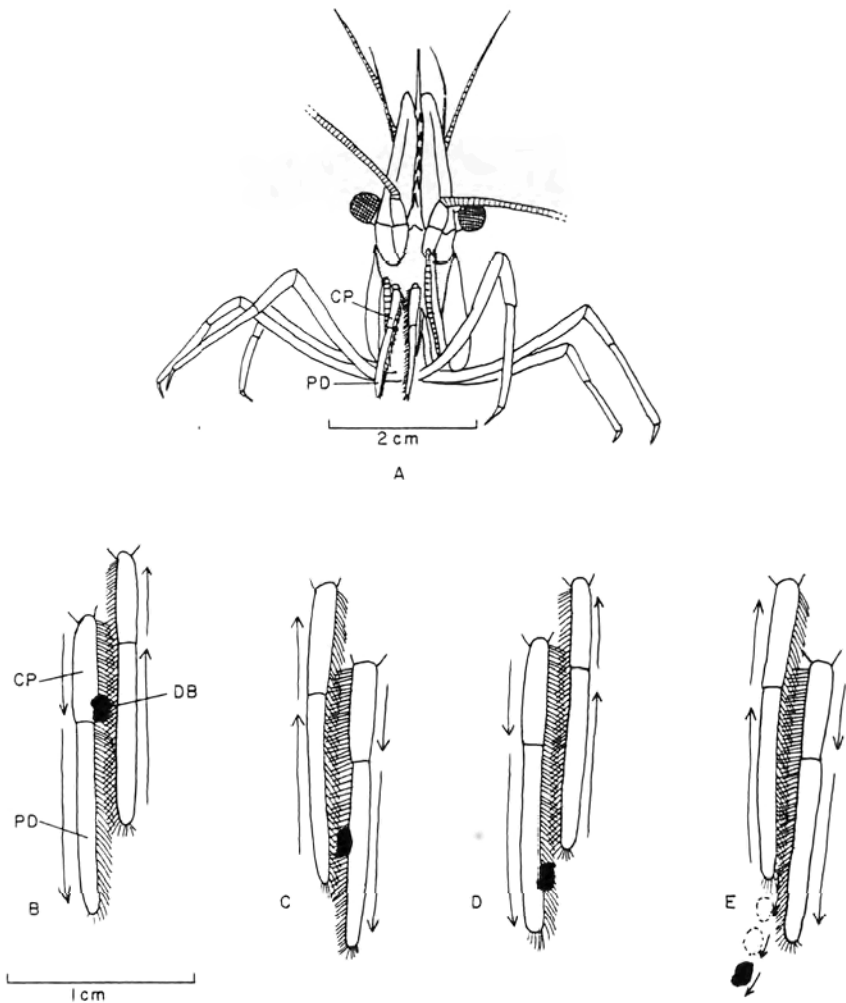


Figure 6. Maxilliped 3 autogrooming: A, anterior view of shrimp at rest; B-E, autogrooming movements clearing macroscopic debris from the cleaning setae of the carpus and propodus-dactylus of maxilliped 3: CP, carpus; PD, propodus-dactylus; DB, debris.

grooming, carpal segments autogroom, while the terminal segments do so after pereopod cleaning, although there is some overlap in both cases.

#### *First pereopods*

Primarily used in probing the substratum for food, the slender first legs perform a minor but specific preening function. These limbs are used in cleaning the antennal flagella and parts of the third maxillipeds. Although the first pereopods of most caridean shrimp are chelate, the dactylus of *P. danae* is vestigial and fused to the propodus, so that there is functionally only one segment.

Two groups of setae on this limb operate as scraping devices. A dense brush of primarily serrate setae is located medially on the proximal end of the

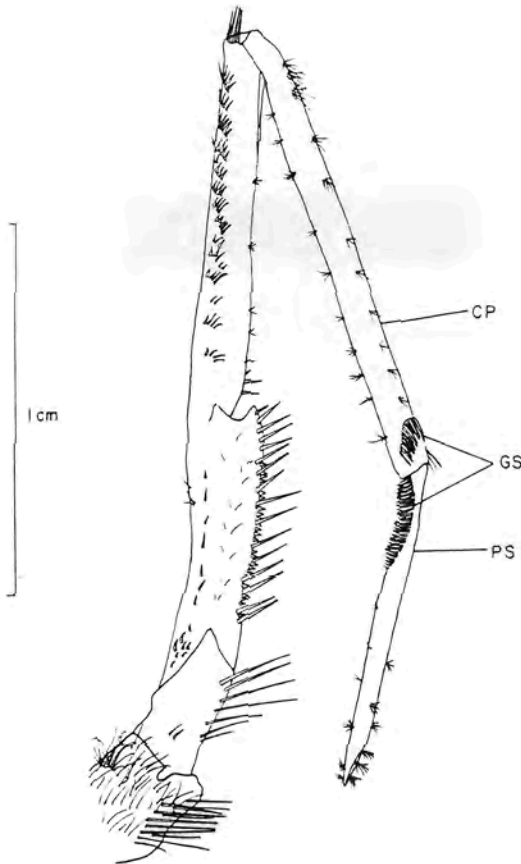


Figure 7. Left first pereopod, medial view: CP, carpus; GS, setal groups specialized for grooming; PS, propodus.

propodus (Fig. 7, Plate 3A-C). Considerable variation in setal shape and size is encountered within this brush. Setae are short and stout ventrally, increasing in length dorsally, and lie parallel to the long axis of the propodus. Ventral-most setae are equipped with scale-setules (Plate 3D), but most of the setae in the brush bear a double row of tooth-setules only (Plate 3C). Setae in the upper rows are large and sickle-shaped, overlapping more ventral setae (Plate 4A). A second group of presumed grooming setae assumes a "V" shape on the dorsal-medial tip of the carpus (Plates 3A and 4A).

Antennal flagella of *P. danae* are groomed by combined action of the first pereopods and third maxillipeds. The flagellum of one side swings forward on its peduncle so that it points somewhat anteriorly. Reaching up with the slightly parted third maxillipeds and first pereopod of the same side, the shrimp hooks the base of the flagellum with the carpal-propodal joint of the first pereopod (Fig. 8A). The propodus is flexed and rotated somewhat medially on the carpus in order to accomplish this. By lowering the first pereopod in this position, the proximal section of the propodus slides down along the length of the flagellum. This draws the flagellum down between the third maxillipeds (Fig. 8B). As the first pereopod is lowered, so are the third maxillipeds; next, the flagellum is elevated back towards its original position. Since it is being held

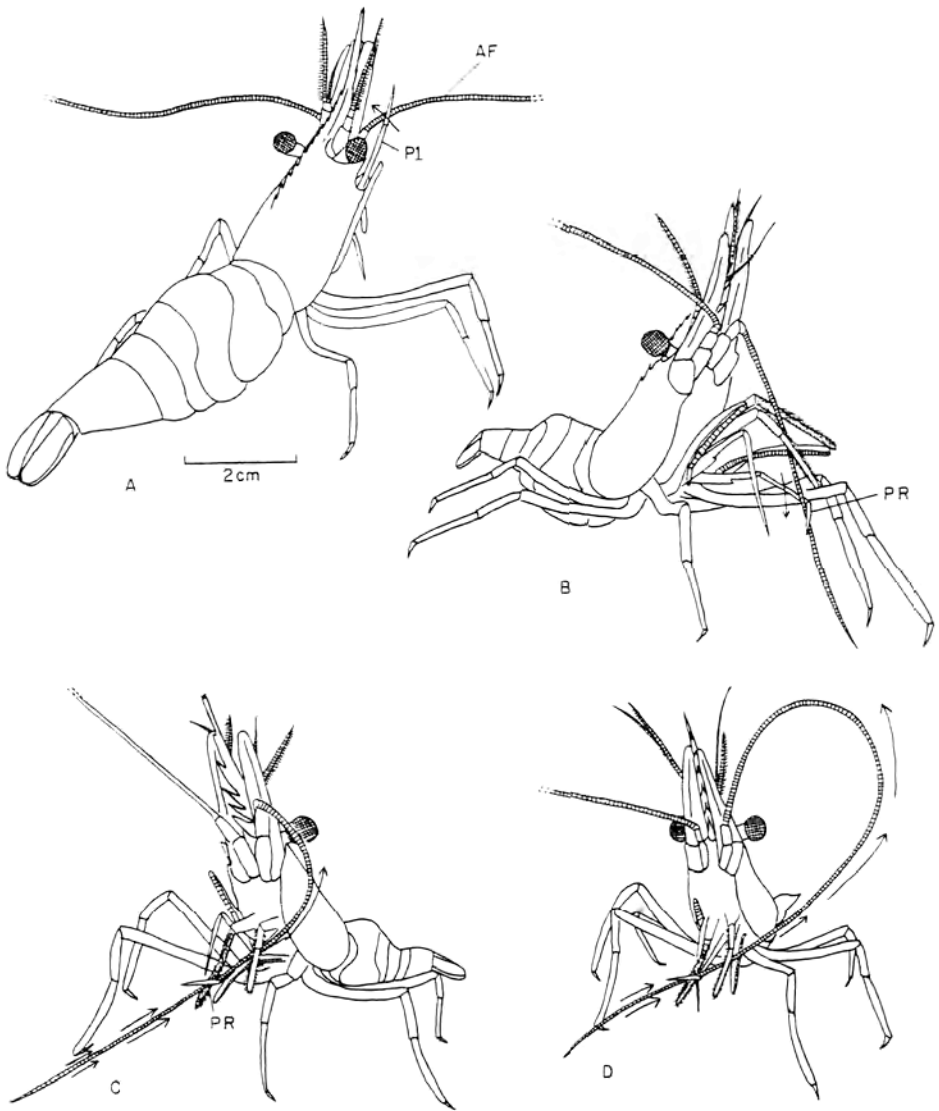


Figure 8. Cleaning of an antennal flagellum: A, pereopod 1 hooking onto the base of the flagellum; B-D, flagellum being drawn through the setal brushes of pereopod 1, maxilliped 3: AF, antennal flagellum; P1, pereopod 1; PR, propodus of pereopod 1.

down by the first pereopod, it forms a characteristic loop in doing so (Fig. 8C, D). The flagellum passes through the rows of grooming setae on the third maxillipeds as it loops dorsally. The third maxillipeds then autogroom. Scraping of the flagellum is accomplished by both the propodal brush of the first leg and the maxilliped rasps. Antennal cleaning usually consists of a few acts, occurring alone or interspersed with antennular and pereopod grooming.

The first pereopods occasionally reach around the third maxillipeds and rub their lateral surfaces both with the propodal brush and also with the tip of the carpus, presumably bringing into play the "V" shaped group of serrate setae described above. Animals with the third maxillipeds removed will swipe and

rub briefly at the walking legs and occasionally this appears to be the case in the intact animal. These limbs may assist the third maxillipeds in pereopod cleaning, but the incompleteness in their movements indicate that this is of minor significance to the animal.

### *Second pereopods*

The second legs of *P. danae* are unequal in size, the left leg being more slender and a third or half as long again as the right (Berkeley, 1928). Otherwise, both limbs are similar in morphology and distribution of setae (Fig. 9A, B). This appendage is chelate, and the fingers of the chelae bear tufts of setae. As in many caridean groups, the carpus is subdivided into a series of segments capable of articulating with each other. Near the proximal end of the carpus, the joints are replaced by annulations of the integument which do not contain individual bundles of flexor and extensor muscles as do the articulating joints (Berkeley, 1928). When not in use, the limbs are folded and carried in front of the shrimp (Fig. 1).

The multi-articulate nature of the carpus makes this segment extremely flexible; the carpus can be twisted into a variety of shapes and is sometimes even thrown into a coil. The utility of this freedom of movement becomes apparent during food-searching movements but particularly when the limbs are grooming. Preening is done by the chela. Moving rapidly over the exoskeleton, it rubs and picks at its surface. Tips of the chelae meet together very tightly, due to a locking device at the terminal end of the fingers. Flanking the tip of the moveable finger are a pair of conical simple setae between which fits a similar single seta on the tip of the fixed finger (Plate 5A, B). Tight closure of the fingers by the setal lock prevents them from slipping on one another. Shrimp can probably pick up very small objects with this chela. Setae in the tufts on the fingers do not appear as if they could be very effective as scrapers or rasps, like the setae on the third maxillipeds. The setae have various degrees of setulation, most being apparently smooth, others having a few scale-like setules. Scanning electron microscopy of the apparently simple setae shows the outline of scale setules on the setal shaft that have never lifted off its surface to form actual setules (Plate 5C, D). The second pereopods of *P. danae* clean a limited area relative to other carideans, such as palaemonids and hippolytids, which brush the gills and brooded eggs with similar groups of setae (Doflein, 1910; Phillips, 1971; pers. obs.). Homologous setae have accordingly much more complex setulation in these groups (Plate 5E). Terminal segments of the first pereopods of *P. danae* (used in searching for food) are equipped with tufts of setae like those on the chelae—this seta may have a purely sensory function in this shrimp.

Pereopods 2 clean the cephalic area of the animal, i.e., the dorsal spines, rostrum, eyes, antennal scales, antennular peduncles. Frontal areas (mouthfield), the walking legs, the ventral edge of the branchiostegite, underside of the thorax—areas with complex topography, i.e., edges and crevices—are preened by these limbs (Fig. 10A-C). When a chela is preening a spot on the body, it may pick and tug at the spot or may open and close the chela rapidly over the spot. Chelipeds will generally clean a small circular area by slight changes in the shape of the carpus. With larger changes in the shape of



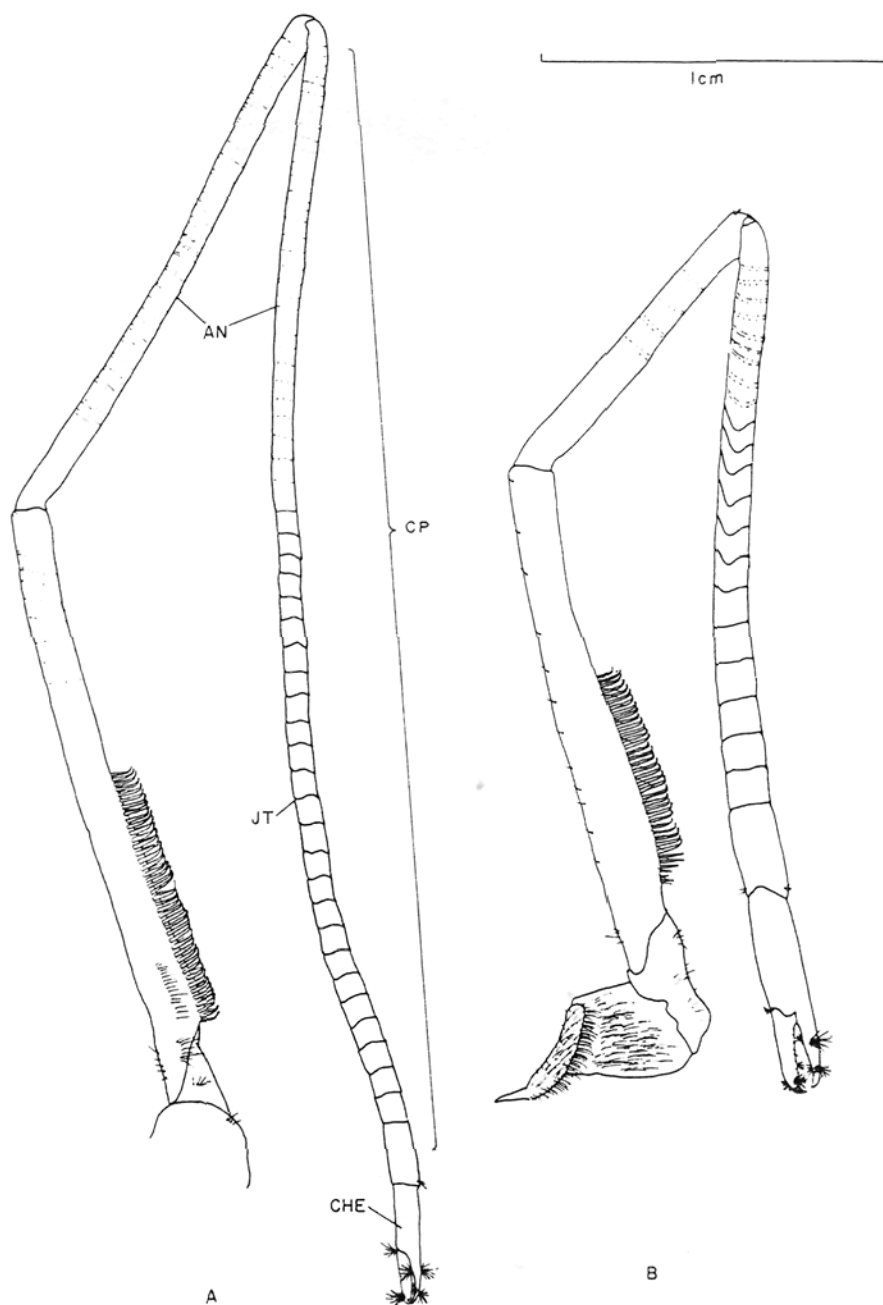


Figure 9. Chelipeds of *Pandalus danae*: A, left cheliped, medial view; B, right cheliped, lateral view: AN, annulation; CHE, chela; CP, carpus; JT, joint.

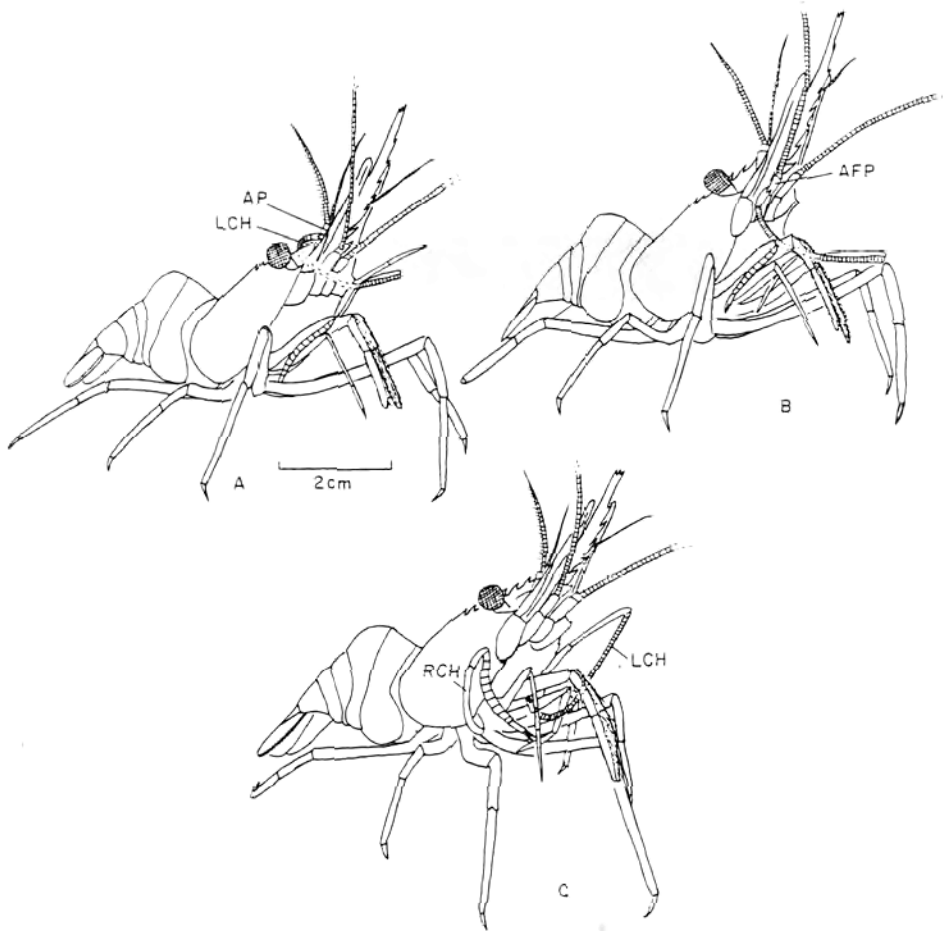


Figure 10. Preening activities of the chelipeds: A, left cheliped picking at right antennular peduncle: B, base of the antennal flagellum: C, left cheliped preening proximal portion of maxilliped 3, right cheliped cleaning pereopod 1: AP, antennular peduncle: AFP, peduncle of antennal flagellum: LCH, RCH, left and right chelipeds.

the carpus and/or movements of the other segments, other areas are reached. *Both chelipeds clean the body, simultaneously or individually.* The two limbs will not only clean on their own side of the body, but one will frequently reach over and groom on the other side of the body along with the other second pereopod. Each cheliped can clean independently, e.g., one may be picking at a walking leg while the other is working at the rostral area. Grooming by these limbs occurs in distinct bouts, in which the shrimp is standing still, and often occurs in conjunction with cleaning of the carapace and abdomen by the fifth pereopod. It is not a frequent behavior as compared to antennular or pereopod cleaning by the third maxillipeds, but the bouts are often much longer in duration, e.g., a half hour or more vs a few seconds or a minute. Antennular, pereopod and antennal cleaning may also occur during these bouts of general *body grooming*.

Unequal sizes of the morphologically similar chelipeds in pandalids seem to be adaptations to behavioral differences. During feeding on a large morsel, the

stronger right second pereopod tears away material and brings it to the mouth many more times than the slender left. Although both limbs preen, if only one limb is preening, it is the longer and more flexible left cheliped. A quantitative analysis of the behavior of both limbs could reveal that differences in length and diameter are related to feeding (right cheliped) and grooming (left cheliped). Neither have become totally specialized for only one kind of activity.

### *Fifth pereopods*

The last pair of walking legs are similar in structure and setation to the anterior two pair; on the distal end of the propodus, however, there are three prominent setal groups not present on pereopods 3 and 4 (Fig. 11A, B; Plate 6A, B). These tufts are dorsomedial, dorsolateral and ventrolateral in position

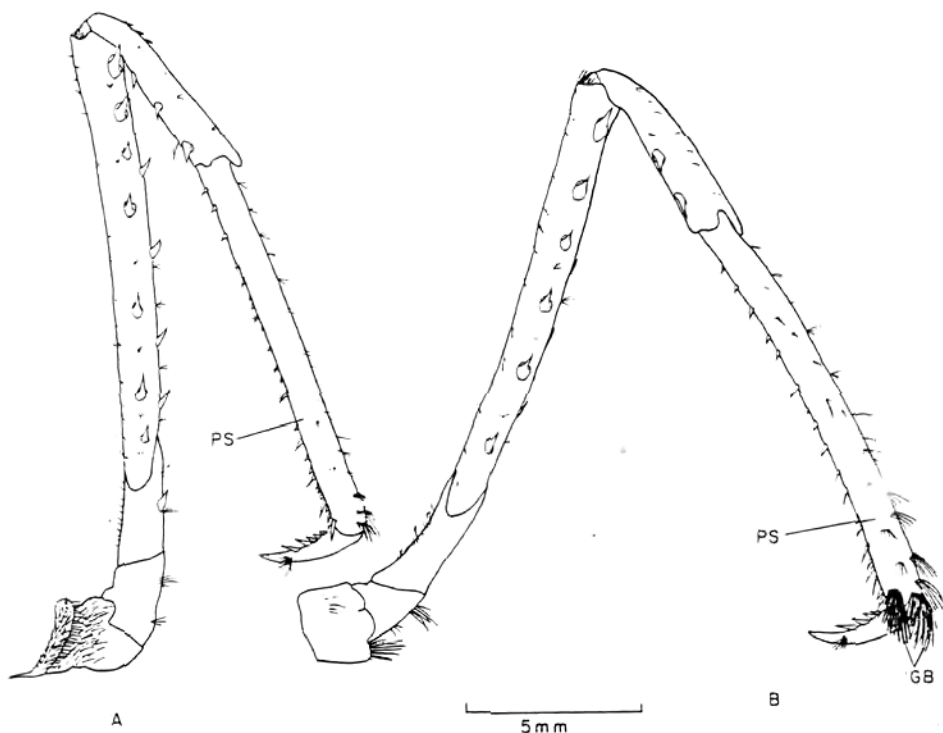


Figure 11. Posterior walking legs: A, right second walking leg (pereopod 4), lateral view; B, right third walking leg (pereopod 5), lateral view; GB, grooming brushes; PS, propodus.

(Plate 6C, D)†. The dorsomedial and ventrolateral brushes are primarily composed of the same type of serrate setae found on the third maxilliped (Plate 7A, B). Setae of the dorsolateral brush, however, lack the tooth setules, and the setal shaft is completely surrounded by scale setules (Plate 8A-C). Scales arise individually and are deeply incised distally, and are lifted well off the surface of the seta. Smaller groups of like setae are located just above the dorsomedial brush, and also along the distal end of the propodus. Homologous

\* In order to apply the terms "medial" and "lateral" to the walking legs, one must imagine the legs as being swung forward so that their longitudinal axes are parallel to the sagittal plane.

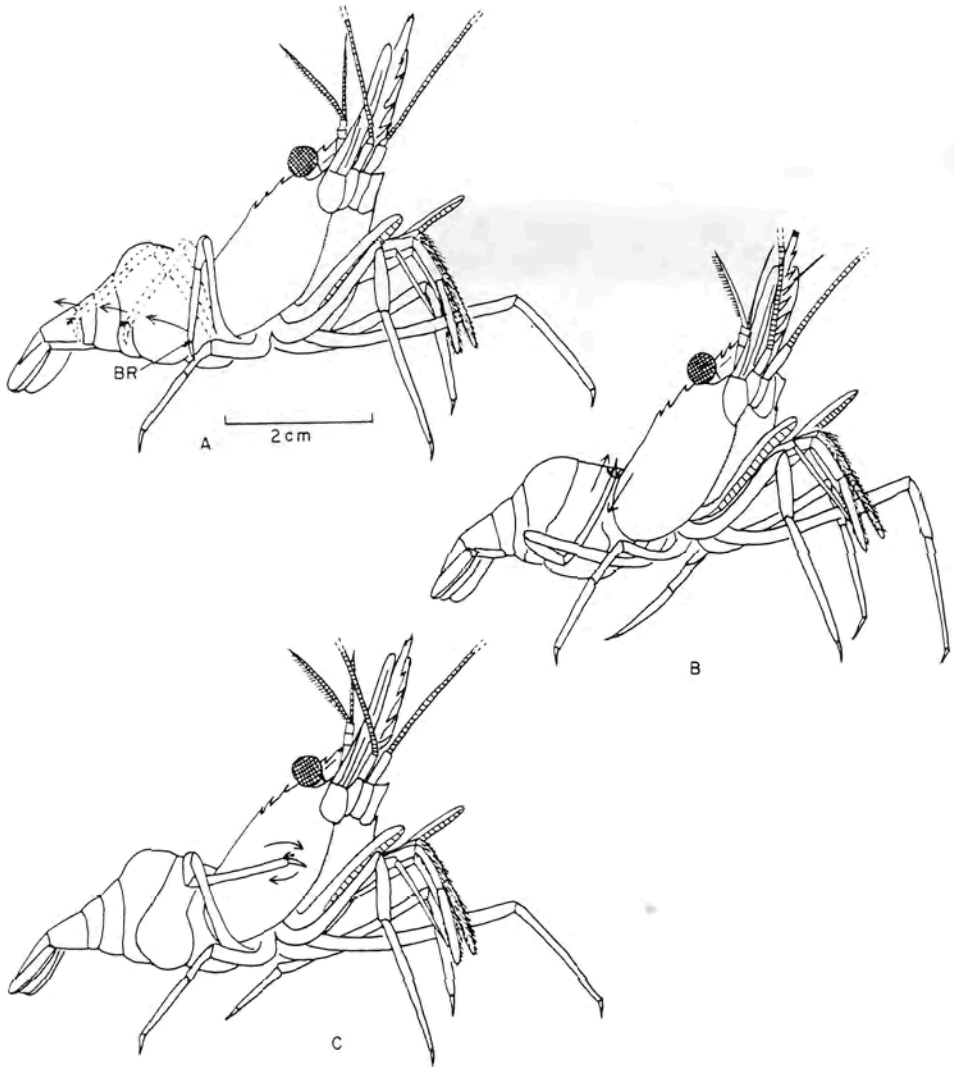


Figure 12. General body grooming by the last walking leg: A, scratching the abdomen; B, rasping the first abdominal segment; C, scouring the carapace; BR, setal brushes on the propodus of the last walking leg.

groups on the other walking legs lack the complex setulation. Setae of the dorsomedial and ventrolateral brushes are short proximally, overlapping the basal portions of longer setae found more distally in the brush (Plate 8D). All of the brushes are elevated off the surface of the limb and project beyond the tip of the propodus. Serrate setae are curved distally, exposing the rows of tooth-setules.

Although the walking legs all have the same musculature (Berkeley, 1928) and articulations, the last leg makes a much wider variety of movements than the anterior two pair; these movements are associated with the use of the grooming brushes on the propodus. The fifth pereopod grooms all of the abdomen, including the pleopods. In cleaning most abdominal surfaces, the

limb is swung back so that the lateral and dorsalateral brushes are in contact with the exoskeleton; the limb appears as an inverted "V" and brushing is accomplished by extending the arms of the "V" apart, with a recovery stroke of flexion (Fig. 12A). By varying the plane in which the limb lies, all parts of the abdomen can be reached, e.g., to clean the pleopods the "V" is stretched out in a frontal plane. Shrimp frequently accommodate cleaning of the posterior terga and tail fan by flexing the tip of the abdomen far forward beneath the body. Scratching is a rapid back and forth motion, bilateral or unilateral. A rotary or scouring movement is also made by the fifth pereopods. Setae are rarely broken, due to the flexible articulation at their bases. In order to clean the anterior segments of the abdomen and the carapace, the limbs assume a position somewhat like a figure "4" (Fig. 12B, C). Grooming brushes are thus brought into play against the broad smooth expanses of the carapace. By variations in the angle between the segments of the limb, most of the carapace can be reached and scoured. Except for the rapid bilateral scratching of the sides of the abdomen, the grooming by this pair of limbs is quite variable in performance, i.e., the left fifth walking leg can be brushing the abdomen while the right is scrubbing the carapace. Like general grooming by the second pereopods, preening is infrequent but prolonged when occurring. Some casual observations indicate a daily rhythm of general grooming to be present in *Pandalus*. On several occasions many of the shrimp in the laboratory were engaged in general grooming at dusk.

I have never seen a brooding female brush the eggs with the fifth legs (or with the chelate limbs, as in palaemonids, hippolytids, and alpheid), although they clean the pleopods. The brooding behavior I have observed consists only of raising the abdomen and beating the pleopods (fanning behavior, see Phillips, 1971).

*Pandalus danae's* grooming appendages can be separated into two types on the basis of behavior. The third maxillipeds and first pereopods are the "specialists", grooming a relatively restricted area of the body. Their movements show low variability in performance, and bouts are of short duration and high frequency. The fifth pereopods and chelate limbs perform the general grooming, the former cleaning the broad expanses of the body, the latter cleaning areas of complex topography in the cephalothoracic region. Preening acts by these limbs are much more varied in order to carry out the diversified function of general body grooming. Bouts of behavior are prolonged but infrequent. Differences in frequency and duration are related to function. The third maxillipeds and first pereopods clean appendages possessing concentrations of sensory receptors, e.g., taste receptors of the walking legs and antennae, tactile hairs of the antennae, olfactory aesthetascs of the antennule (Laverack, 1968; Barber, 1960). Frequent grooming seems to be necessary to keep sensory surfaces operating. General grooming, on the other hand, could be performed to keep the animal free from being encumbered with an epibiota that weighs it down or interferes with locomotion. Experimental work discussed below deals with these hypotheses.

Some overlap of preening by the limbs occurs. Pereopod 2 can pick at the smooth surfaces of the carapace, although pereopod 5 usually scours there. *Pereopods 2 pick and tug at the other pereopods, while the third maxillipeds sweep over them.*

## EXPERIMENTS

The general question being tested by experimental work at Friday Harbor was whether or not grooming by the appendages keeps the shrimp's exoskeleton free of epizoic and sediment fouling. Shrimps were prevented from preening by removing cleaning legs in various combinations. Exposure to spores and larvae of settling organisms occurred in cages set out in the animal's natural environment.

Appendages were removed by grasping them with forceps close to the basi-ischial joint and pulling gently until the limb broke off at the natural breakage plane, minimizing blood loss and danger of infection. The third maxillipeds, however, did not usually detach as easily and were cut off near the coxa. Cages were cylindrical drums of  $\frac{1}{4}$  inch (0.65 cm) hardware cloth, 36 inches (91.5 cm) long, 11 inches (28 cm) in diameter. Ends were covered with fine plastic screening. A 6 x 12 inch (15.25 x 30.5 cm) asbestos board settling plate was hung from most cages. These plates were intended to sample biota settling out in the vicinity of the cages—to check for differential settlement between the shrimp's exoskeleton and an inanimate substrate. Cages with experimental and control animals were lowered along the floating docks at Friday Harbor among algae (*Laminaria*) which was also placed inside as a substrate for the shrimp. Food was supplied periodically (chicken necks, fish scraps).

Two major ablation experiments were performed. Duration of the first (general grooming experiment) was 29 days; it was composed of four treatments, each differing in the pair of appendages removed: (1) last walking legs, (2) chelate limbs, (3) both previous pairs, (4) first walking legs (control). The antennular cleaning experiment had two groups; those with no third maxillipeds (experimentals) and controls (no ablation). These shrimp were exposed in cages for 10 days. At the end of the tests, animals were killed and preserved, along with the settling plates, in 10% buffered seawater formalin.

## RESULTS

*General grooming experiment*

Examination of experimental animals revealed a conspicuous infestation of all parts of the body by a large epizoic suctorian, *Ephelota* sp. (probably *E. gemmipara* Hertwig, kindly identified by Dr Eugene Kosloff, Friday Harbor Laboratories). Qualitatively, treatment 3 shrimp (pereopods 2 and 5 removed) showed the heaviest fouling; control animals exhibited little or no fouling. Metazoan fouling was rare, although a few treatment 3 shrimp had hydroid colonies (*Obelia* sp.) growing on the cephalothorax, which was quite extensive in one case. Suctorians on control animals were rare. Microscopic investigation of the exoskeleton revealed the presence of stalked ciliates and other suctorians in all animals. In order quantitatively to compare the degree of fouling between treatment (non-grooming) and control (preening) animals, *Ephelota* was chosen as a test organism. A number of shrimp were chosen at random from each treatment and designated parts removed from all sections of the body for

counting. So that molting would not be a variable, only animals which had not molted were used. Non-molters were identified by characteristics of the amputated limb bud, and presence or absence of scabbing about the base of the limb due to incidental injuries during limb removal. Body parts examined were: ventral surface, exopod of right uropod; dorsal surface, endopod of right uropod; second right abdominal pleura; posterior half of carapace on right side; fourth pereopod; dorsal spines; and rostrum. Length and width of each piece was measured in a prescribed manner to give an approximation of area. The number of suctorians per  $\text{mm}^2$  was determined and the median number for each treatment is given in Table 1.

Table 1. Median number of *Ephelota*/ $\text{mm}^2$  growing on different parts of animals in the general grooming experiment

	Ventral surface, exopod of uropod	Dorsal surface, endopod of uropod	2nd abdominal pleura	Carapace section	4th pereopod	Rostrum	Dorsal spines	N
Tr1*	0.122	0.071	0.022	0	1.00	0	0.015	15
Tr2	0.010	0	0	0.009	1.282	0.296	0.194	8
Tr3	0.282	0.286	0.086	0.038	1.35	0.50	0.444	15
Control	0	0	0	0	0.20	0	0	15

- \* Tr1, last walking legs removed; chelipeds present.  
 Tr2, last walking legs present; chelipeds removed.  
 Tr3, last walking legs and chelipeds removed.  
 Control, first walking legs removed.

The rank sum test (Wilcoxon T test, Mann-Whitney U test) was used to determine whether observed differences in suctorian fouling between experimental and control shrimp were statistically significant. Under the hypothesis being tested, it is expected that the number of suctorians on a given body part should be greater in the treatments where the shrimp could not groom that section of the body (cleaning limb ablated) than in the treatments where preening took place. Based on the behavioral observations, pereopod 2 preens the cephalic area, walking legs and other cephalothoracic regions of intricate topography. Pereopods 5 groom all abdominal areas and the smooth expanses of the carapace. Thus, some cephalic area should show fouling in treatment 2 and 3 shrimp, with comparatively little settlement in treatment 1 and control animals, which possess the limbs that preen this region. Table 2 gives the comparisons between treatments and control, with Table 3 showing the results among treatments.

In general, the tests between treatments and control support the hypothesis that the grooming limbs can prevent settlement of an epizoite. Agreement is not quite as good in the between-treatment tests, but the discrepancies might be attributed to behavior not directly observed. It was assumed that the last walking leg cleaned the smooth surfaces of the carapace, although some overlap in this area with pereopod 2 was noted in the behavioral observations. The almost complete disagreement found in test 4 (carapace) section in Tables 2

Table 2. Comparison of suctorian fouling between treatment and control animals. Probabilities (computed by the rank sum test) are the likelihood that the median # suctorians/mm<sup>2</sup> are not different;  $P \leq 0.05$  are considered significant

Test	Hypothetical result	Experimental result	$p$	Agreement between hypothetical and experimental results
<i>(1) Ventral surface, exopod of uropod</i>				
Tr1 vs con*	Tr1 $\neq$ con	Tr1 $\neq$ con	$\leq 0.01$	+
Tr2 vs con	Tr2 = con	Tr2 = con	$> 0.20$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$\leq 0.01$	+
<i>(2) Dorsal surface, endopod of uropod</i>				
Tr1 vs con	Tr1 $\neq$ con	Tr1 $\neq$ con	$\leq 0.01$	+
Tr2 vs con	Tr2 = con	Tr2 = con	$> 0.20$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$< 0.01$	+
<i>(3) Second abdominal pleura</i>				
Tr1 vs con	Tr1 $\neq$ con	Tr1 $\neq$ con	$0.01 < P < 0.05$	+
Tr2 vs con	Tr2 = con	Tr2 = con	$> 0.20$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$< 0.01$	+
<i>(4) Carapace section</i>				
Tr1 vs con	Tr1 $\neq$ con	Tr1 = con	$0.10 < P < 0.20$	-
Tr2 vs con	Tr2 = con	Tr2 $\neq$ con	0.05	-
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$\leq 0.01$	+
<i>(5) Rostrum</i>				
Tr1 vs con	Tr1 = con	Tr1 = con	$> 0.20$	+
Tr2 vs con	Tr2 $\neq$ con	Tr2 $\neq$ con	$< 0.01$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$< 0.01$	+
<i>(6) Dorsal spines</i>				
Tr1 vs con	Tr1 = con	Tr1 = con	$0.10 < P < 0.20$	+
Tr2 vs con	Tr2 $\neq$ con	Tr2 $\neq$ con	$0.01 < P < 0.05$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$\leq 0.01$	+
<i>(7) Second walking leg</i>				
Tr1 vs con	Tr1 = con	Tr1 = con	$0.10 < P < 0.20$	+
Tr2 vs con	Tr2 $\neq$ con	Tr2 $\neq$ con	$0.01 < P < 0.05$	+
Tr3 vs con	Tr3 $\neq$ con	Tr3 $\neq$ con	$\leq 0.01$	+

\* con, control.

and 3 can be reconciled somewhat if it is assumed that both pairs of limbs clean the area. Treatment 3 shrimp tended to show greater fouling in abdominal areas than treatment 1 animals, although both groups were without the limb that cleans this area. Compensatory cleaning by the chelate limb of the latter group could account for the lower incidence of fouling, although such behavior was never observed in laboratory animals with only pereopod 5 ablated.



Table 3. Comparison of suctorian fouling among treatments

Test	Hypothetical result	Experimental result	P	Agreement
(1) <i>Ventral surface, exopod of uropod</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 ≠ Tr2	≤ 0.01	+
Tr1 vs Tr3	Tr1 = Tr3	Tr1 ≠ Tr3	0.01 < P < 0.05	-
Tr2 vs Tr3	Tr2 ≠ Tr3	Tr2 ≠ Tr3	≤ 0.01	+
(2) <i>Dorsal surface endopod of uropod</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 ≠ Tr2	< 0.01	+
Tr1 vs Tr3	Tr1 = Tr3	Tr1 ≠ Tr3	0.01 < P < 0.05	-
Tr2 vs Tr3	Tr2 ≠ Tr3	Tr2 ≠ Tr3	≤ 0.01	+
(3) <i>Second abdominal pleura</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 = Tr2	0.05 < P < 0.10	-
Tr1 vs Tr3	Tr1 = Tr3	Tr1 ≠ Tr3	0.05 < P < 0.10	-
Tr2 vs Tr3	Tr2 ≠ Tr3	Tr2 ≠ Tr3	0.01 < P < 0.05	+
(4) <i>Carapace section</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 = Tr2	P > 0.20	-
Tr1 vs Tr3	Tr1 = Tr3	Tr1 = Tr3	< 0.01	-
Tr2 vs Tr3	Tr2 ≠ Tr3	Tr2 = Tr3	0.05 < P < 0.10	-
(5) <i>Rostrum</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 ≠ Tr2	< 0.01	+
Tr1 vs Tr3	Tr1 ≠ Tr3	Tr1 ≠ Tr3	< 0.01	+
Tr2 vs Tr3	Tr2 = Tr3	Tr2 = Tr3	> 0.20	+
(6) <i>Dorsal spines</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 = Tr2	= 0.10	-
Tr1 vs Tr3	Tr1 ≠ Tr3	Tr1 ≠ Tr3	≤ 0.01	+
Tr2 vs Tr3	Tr2 = Tr3	Tr2 = Tr3	0.05 < P < 0.10	+
(7) <i>Second walking leg</i>				
Tr1 vs Tr2	Tr1 ≠ Tr2	Tr1 = Tr2	> 0.20	-
Tr1 vs Tr3	Tr1 ≠ Tr3	Tr1 ≠ Tr3	= 0.05	+
Tr2 vs Tr3	Tr2 = Tr3	Tr2 = Tr3	> 0.20	+

### *Antennular grooming experiment*

Removal of the third maxillipeds from *Pandalus* results in a noticeable discoloration of the outer flagellum of the antennules within a few days. Experimentals and controls kept in cages off the Friday Harbor pier for ten days were preserved and the antennules examined microscopically. Darkening of the outer flagellum on experimental animals was due to the growth of suctorians, sessile ciliates, *Ephelota*, an erect bryozoan and especially benthic diatoms on the aesthetascs. Debris was lodged between the bases of the aesthetascs. One of the experimental antennules was given to Dr Richard Norris, University of Washington algalogist, for identification of the diatoms. *Synedra tabulata* (Ag.) was the most common diatom on the olfactory hairs, with the genera *Licmophora*, *Cocconeis*, *Melosira*, *Biddulphia*, *Hyalodiscus*,

*Navicula*, *Grammatophora*, and also germinating brown algal spores being present. Diatoms were occasional on the aesthetascs of control animals, but infestation was negligible when compared to the experimentals (Plates 9 and 10). An exception to the above was found in bryozoan settlement. Three of ten control antennules had bryozoan colonies growing on the aesthetascs, while only two of ten experimentals had them. In most cases, there were less than ten colonies on any antennule, with the exception of one control (20). *Ephelota* was more abundant on the inner and outer flagella of experimentals, but was found growing on the flagella proper, not on the olfactory hairs. SNOW (1970) has reported fouling of the antennules of *Pagurus alaskensis* (Benedict) with diatoms and dirt when the endopod of the third maxilliped is removed.

Compensatory grooming did appear in this experiment. Animals without the third maxillipeds in the laboratory lowered the antennule as in a cleaning act. The first pereopods would reach and quickly rub some part of the antennule. This behavior was never prolonged and the size of the cleaning brushes of the first leg is quite small relative to those on the third maxillipeds. As the results of the third maxilliped ablation experiments show, this behavior did not have much effect in keeping the antennules free of fouling.

Diatoms occurred on other surfaces of the exoskeleton of both experimental and control animals in both experiments. They were not very abundant and qualitatively did not differ in this respect between experimentals and controls. The antennules are constantly flicked back and forth by the animal so that circulation of water about the aesthetascs is greater than most other exoskeletal surfaces, perhaps ameliorating the environment for diatoms in some manner.

Settling plates had little macroscopic growth developed. A green slick composed of heavy diatom growth was the most noticeable fouling observed. Careful examination of the plates revealed small numbers of newly-metamorphosed balanoid barnacles, serpulid and spirorbid worms, and the hydroid *Obelia*. Density of these organisms was quite low—approximately  $0.08/\text{cm}^2$  was the highest density for any of these animals (newly-metamorphosed barnacles).

#### DISCUSSION

Ablation experiments have demonstrated differential settlement of epizoic organisms on grooming and non-grooming *P. danae*. Suctorians and diatoms were most abundant, the former occurring on all parts of the body, with the latter showing high densities on non-preened antennules. Significantly higher densities of *Ephelota* on non-grooming shrimp shows that the scraping and rasping of the exoskeleton by setal brushes on certain thoracopods does remove or keep the protozoans from settling on *P. danae*. Macroscopic fouling was light, restricted to the hydroid *Obelia* on a few treatment 3 animals. The duration of the experiment was not long enough for development of more extensive fouling. Settling plates attached to experimental and control cages were irregularly covered with a film of microorganisms (bacteria, diatoms, protozoans). Settlement of macroscopic animals (barnacles, hydroids, tubicolous polychaetes) was very low. Thus, growth on non-grooming shrimp and the settling plates was quite similar. O'Neill & Wilcox (1971), working at

Point Hueneme, California, pointed out that bacteria and diatoms settle first on virgin surfaces, while Scheer (1945) found the former plus protozoans and hydroids (including *Ephelota* and *Obelia*) and also bryozoans on newly exposed settling plates in Newport Bay. *Pandalus danae* exposed for longer periods without cleaning should develop a more extensive fouling community on its body. Although molting completely frees the shrimp of epibionts, periods between molts are prolonged during winter months and cannot occur when females are brooding eggs (October-April, Berkeley, 1930; to May-June, pers. obs.).

Epizoic growth on non-cleaning *P. danae* indicates the selective pressures operating on the animal which have brought about the evolution of grooming setae and preening behavior. Fouling organisms must have interfered with a wide variety of vital activities of the shrimp so that rudimentary preening behavior would have a selective advantage. Certainly, the larvae and spores of settling animals and plants have always been a part of the crustacean environment. The hard chitinous exoskeleton of decapods is a suitable substrate for sessile organisms; many macrurans and brachyurans, which do not groom as vigorously as natantians and anomurans, carry fouling organisms on their bodies. The hypothesis that settlement of epibionts is deleterious and is responsible, in part, for grooming behavior must be supported by evidence that fouling decreases the probability of survival and/or reproductive success. Eldred (1962) reported that barnacle fouling of the penaeid shrimp *Sicyonia dorsalis* Kingsley occurred mainly along the dorsal midline of carapace and abdomen, with some barnacles located between abdominal segments. Similarly, barnacles settling on *Penaeus setiferus* L. (Dawson, 1957) were positioned on the dorsal midline of the tail. Penaeid shrimp do clean with their chelate legs (personal observation on *Gennadas* sp.); the mid-dorsal position of the barnacles given above could be due to the inability of penaeids to groom that area efficiently or perhaps is a result of an injury preventing cleaning. The added weight and the frictional forces generated by these epizoites must interfere with swimming, increasing the chances of predation. The large stalked suctorians settling on *Pandalus* must produce some frictional drag during swimming much as the fouling organisms growing on hulls of ships and boats do, decreasing the efficiency of locomotion. A more extensive growth of settlers, such as the barnacles fouling the penaeids, would certainly have this effect. Growth of epibionts between segments of the body and joints of limbs would prevent bending in areas of articulations, impeding vital movements. In *P. danae*, concentration of *Ephelota* on the walking legs of non-cleaning animals was greatest around the joints; growth of a larger animal in these positions could prevent normal ambulation.

Regular cleaning of pereopods, antennae and antennules undoubtedly maintains sensory sites on these appendages. Mechanoreception is dependent on deflection of setae by an external force (Laverack, 1968); clogging of such a sensory seta by debris or a fouling organism would interfere with its function. Contact between the stimulating molecule and the receptor site is necessary for chemoreception; if sediment or a settling organism covers a receptor, vital information about the animal's surroundings could be lost. Behavioral evidence indicates that chemoreceptors are located on the dactyls and chelae of the pereopods, and on the antennae and antennules of crustaceans (Barber, 1960).

Chemoreceptors have been demonstrated electrophysiologically on the dactyls of crab pereopods (Case, 1964), on the antennules of lobsters (Laverack, 1964), crayfish (Hodgson, 1958), crabs (van Weel & Christofferson, 1966), and shrimp (Ache & Case, 1969). Studies on the ultrastructure and permeability of the cuticle of the antennular aesthetascs of *Pagurus hirsutiussculus* Dana (Ghiradella *et al.*, 1968) further indicate the olfactory nature of these setae.

Debris on the pereopods and both pairs of antennae is removed by the third maxillipeds and first pereopods of *P. danae*. An absence of antennular grooming by experimental animals resulted in significant fouling of aesthetascs by diatoms and particulate matter within ten days. Olfaction could be impaired by reduction of aesthetasc surface or by interrupted circulation of water through the aesthetasc rows. Olfaction is important to crustaceans in finding food and, in some cases, finding a mate via a pheromone. Loss of this faculty due to fouling would seriously affect the animal's chances of contributing genes to subsequent generations.

The eyes are kept clean by the chelipeds (removal of epizoites) and by a convulsive twitching of the eyestalks, which keeps fine sediment from settling. Facets of the eyes must be kept free from fouling so that light can penetrate through and strike the light sensitive elements within the ommatidia. Unimpeded vision is necessary for orientation in the environment and detection of movements signalling the presence of predators or prey.

#### ACKNOWLEDGEMENTS

Space, facilities and assistance were generously given by the Director and staff of the University of Washington's Friday Harbor Laboratories without which this work could not have been possible. Financial assistance was provided by a Grant-in-Aid of Research from the Society of Sigma Xi.

I am grateful to Drs Abraham Fleminger and Robert R. Hessler for suggestions and helpful discussion and especially to Dr William A. Newman for his useful comments on the manuscript and invaluable advice during the course of this work.

I wish to thank Ms Virginia L. DeCamp for her valuable assistance in the preparation of the manuscript.

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## ADDENDUM

Emphasis in this paper has been placed on the relationship between the serrate and multiscaled form of grooming setae and their rasping function. However, Farmer (1974), in a recent report on the functional morphology of *Nephrops norvegicus* (L.) (Astacura: Nephropidae), has taken the view that serrate setae on the mouthparts and cleaning limbs are primarily chemosensory. Large tooth setules of these setae presumably increase the surface area available for stimulation. This hypothesis is based on the electrophysiological work of Shelton & Laverack (1970) on the chemoreceptive nature of certain setae of *Homarus gammarus* (L.). Their results show that several types of setae are chemosensory; serrate setae of mouthparts, "squat hairs" from the inner edges of the second and third chelate pereopods, and serrulate setae from the dactyls

of the achelate walking legs. Thus, setae of highly differing morphologies (including the aesthetascs) have chemosensory capabilities. However, tooth setules of serrate setae appear not to be primarily chemosensory in function, but rather are adaptations for gripping, scraping, abrading and cutting. If surface area is very important in determining the structure of a primarily chemosensory seta, then a form like that of the villous "squat hairs" would be more adaptive. Furthermore, even if the teeth were permeable to chemical stimuli, their interiors would have to be confluent with the lumen of the setal shaft to accommodate nerve endings. Sections of serrate setae of crayfish (Thomas, 1970) indicate that the teeth are solid; the broken subsetules of scales found on multiscaled setae of *Pandalus* indicate they too are solid (Fig. 8C).

Examination of setae from the dactyls of the last two pairs of walking legs of *Homarus americanus* H. Milne-Edwards reveals that those from the penultimate pair are serrulate, like those figured in Shelton & Laverack (1970, fig. 2A) while those of the last pair are strongly serrate. The setae on the latter are identical with setae found in the propodal brushes of the same two pair in *Homarus* and *Nephrops* (those of *Nephrops* figured and described by Farmer, 1974). The last leg is used extensively by nephropideans in grooming the abdomen and pleopods, and thus differences in the morphology of setae from the dactyls of pereopods 4 and 5 appear to be correlated with cleaning. Farmer (1974) does state that serrate setae from the propodal brushes of legs 4 and 5 may be partially associated with grooming. However, it is clear that the complex tooth and scale setulation are primarily adaptations to rasping and scraping.

Among caridean shrimp, complexity of setulation increases in setae used for grooming. Setae on the cleaning chelae of carids, which are used to brush their gills, bristle with complex scale setules (e.g., palaemonids, hippolytids). Those on the chelae of shrimp which do not clean their gills lack them (e.g., *Pandalus*). Grooming chelae are also used in finding and taking food so that their setae may also possess chemosensory capabilities—yet the degree of scale setulation in setal tufts varies positively with grooming behavior. The propodus of the last walking leg of most carideans has a serrate setal brush developed to some extent. All walking legs respond to food stimuli, yet the anterior two pair have no such brush of setae. Observations on the use of this cleaning brush show the serrate setae being scraped against the exoskeleton. Serration of setae on other appendages of decapods can be related to other, non-sensory functions (Thomas, 1970; Fryer, 1960). Yet all of these serrate setae could concomitantly be chemoreceptive as well.

#### EXPLANATION OF PLATES

##### PLATE 1

Serrate setae on the medial surface of the propodus-dactylus of the third maxilliped:

A. Entire setae (x200).

B. Tip of a serrate seta (x1000).

C. Compound areas of the setal shaft (x500).

D. Medial side of a seta, wing-like pairs of scale setules (x2000): ts, tooth setule; sc, scale setule.

## PLATE 2

Grooming setae from the carpus of the third maxilliped:

- A, B, C. Views giving orientation of setules on the setal shaft.  
 D. Close-up of the complex setules: ss, subsetule.  
 A, (x500); B, (x2000); C, (x2000); D, (x5000).

## PLATE 3

- A. Dorsomedial view of a left first pereopod, carpal-propodal joint (x50).  
 B. Medial view of the propodus, right first pereopod, showing the grooming brush (x50).  
 C. Propodal brush, pereopod 1 (x200).  
 D. Seta from the ventral edge of the propodal brush (x2000): d, distal; cp, carpus; p, proximal; ps, propodus; 3D, seta magnified in D; sk, sickle-shaped seta.

## PLATE 4

- A. Sickle-shaped setae from the dorsal side of the propodal brush, pereopod 1 (x500).  
 B. Upper arm of the "V" shaped group of setae on the distal end of the carpus of pereopod 1, (shown in Plate 3A) (x200).

## PLATE 5

- A. Tip of the right chela, with the setal chela lock at the tips of the fingers (x100).  
 B. Tip of the left chela, viewed from below the movable finger, showing the chela lock and the setal tufts arising from the finger (x200).  
 C. Portions of setae in the tufts of the movable finger of the right chela (location given in A) (x2000).  
 D. Close-up of the upper seta in C, showing the scales lying on the surface of the setal shaft (x11,000).  
 E. Setae from tufts on the first chela of *Palaemon macrodactylus* Rathbun (x500): cl, setae composing the chela lock; ff, fixed finger; mf, movable finger; sc, scale setules; sl, scales; 5C, setae magnified in C.

## PLATE 6

- A. Propodal-dactylar joint of the second walking leg (x50).  
 B. Propodal-dactylar joint of the last walking leg, showing the grooming brushes (x50).  
 C. Dorsomedial brush of a (right) last walking leg (x100).  
 D. Grooming brushes on the lateral surface of a (right) last walking leg (x50): ds, dactylus; dlb, dorsolateral brush; dmb, dorsomedial brush; vlb, ventrolateral brush; ps, propodus.

## PLATE 7

- A. Serrate setae of the dorsomedial brush of the last walking leg (x1000).  
 B. Serrate setae of the ventrolateral brush of the last walking leg (x1000).

## PLATE 8

- A. Multiscaled setae of the dorsolateral brush of the last walking leg (x200).  
 B. Portion of a multiscaled seta, showing the individual scale setules (x 2000).  
 C. Close-up of two scale setules, with broken subsetules (x6000).  
 D. View of the dorsomedial brush projecting from the tip of the propodus, showing curvature of the serrate setae which exposes the tooth setules (x200).

## PLATE 9

- A. Portion of the outer flagellum (antennule) of a control animal, showing the clean aesthetascs (x100).  
 B, C. Aesthetascs of experimental (non-grooming) shrimp, showing fouling by diatoms and debris (x100): aes, aesthetascs; db, debris; dm, diatoms; of, outer flagellum of antennule.

## PLATE 10

- A. Close-up of aesthetascs of a control (grooming) shrimp, showing absence of fouling (x200).  
 B. Close-up of aesthetascs of experimental (non-grooming) shrimp, with epizoic diatoms (x200): aes, aesthetascs; dm, diatoms; of, outer flagellum.

