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The Functional Morphology of the Grooming Appendages of *Palaemonetes kadiakensis* Rathbun, 1902

BRUCE E. FELGENHAUER
DEPARTMENT OF BIOLOGY
FLORIDA STATE UNIVERSITY, TALLAHASSEE

AND

FREDERICK R. SCHRAM
DEPARTMENT OF PALEONTOLOGY
SAN DIEGO NATURAL HISTORY MUSEUM

Competition for attachment surfaces is a constant process in the aquatic environment. Sessile protozoans and various other invertebrates attach to almost any available substrate as epibionts, and the crustacean exoskeleton is such a substrate.

Aquatic Crustacea are often fouled by epibionts and debris. This fouling may cause difficulties in locomotion or inhibit sensory reception depending upon the location and intensity of infestation (Bauer, 1975). Heavy infestations of epibionts at specific locations i.e., pleopods, branchiostegites, gill lamellae, and antennae, could impede normal fluid flow around the animal.

Suspended materials in the water column may clog openings and cover surfaces through which contact between the organisms and the external environment must take place, i.e., gill lamellae, chemoreceptive setation, and antennae (Bauer, 1975). Such epibiont infestation has elicited the development of elaborate cleaning systems.

There are very few reports on crustacean grooming in the literature. Doflein (1910) described gill and exoskeleton grooming by the first cheliped of *Palaemon xiphias*. Needler (1931) observed *Pandalus danae* clean its pleopods before laying eggs. Hoglund (1943) reported cleaning behavior which preceded spawning in

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Palaemon squilla. Bauer (1975) reviewed some earlier work and described in detail the relevant morphology of the preening appendages and grooming behavior of *Pandalus danae.*

This study parallel's Bauer's work, but investigates the morphology and grooming activities of a freshwater prawn, *Palaemonetes kadiakensis* Rathbun, 1902, and constitutes the first observations of grooming in freshwater prawns. Comparisons between the morphology and activities of marine prawns and freshwater prawns is described below.

MATERIALS AND METHODS

Palaemonetes kadiakensis occurs mainly in waters of the central United States west of the Alleghenies (Holthius, 1949). The prawn is transparent and ranges up to 54 mm. in total body length.

Collections were made by dip netting in the shallows of Lake Charleston, Coles County, Illinois. Prawns were placed in aquaria with a sample of natural substrate and plants. Observations of grooming behavior were recorded at time intervals around the clock. Setal structure of the pereiopods were analyzed by light and scanning electron microscopy. For SEM examination, whole prawns were fixed in 4 per cent glutaraldehyde in .1 molar phosphate buffer. Then, after a rinsing of the appendages, the specimens were fixed an additional 4 hr. in 4 per cent glutaraldehyde alone and afterward rinsed in a .1 molar phosphate buffer. Appendages were dried in a CO_2 critical point dryer, sputter coated with carbon, and then sputter coated with 10-15 nm of gold paladium. Observations were made on a JEOL-JSM-35 SEM at 5 kilovolts. Drawings in Figure 1 were made with a Wild Camera Lucida and drawings in Figure 2 were generally made from photographs.

APPENDAGES

The functions of each appendage in grooming were observed and recorded. The first, second, and fifth pereiopods (fig. 1b,c,f), along with the third maxillipeds (fig. 1a), are responsible for keeping the body and sensory areas free from fouling materials. The third and fourth pereiopods (fig. 1d,e) are devoid of any functional grooming setation, but support the prawn during grooming.

The first, second, and fifth pereiopods were observed to clean specific locations on the exoskeleton, and are armed with specialized

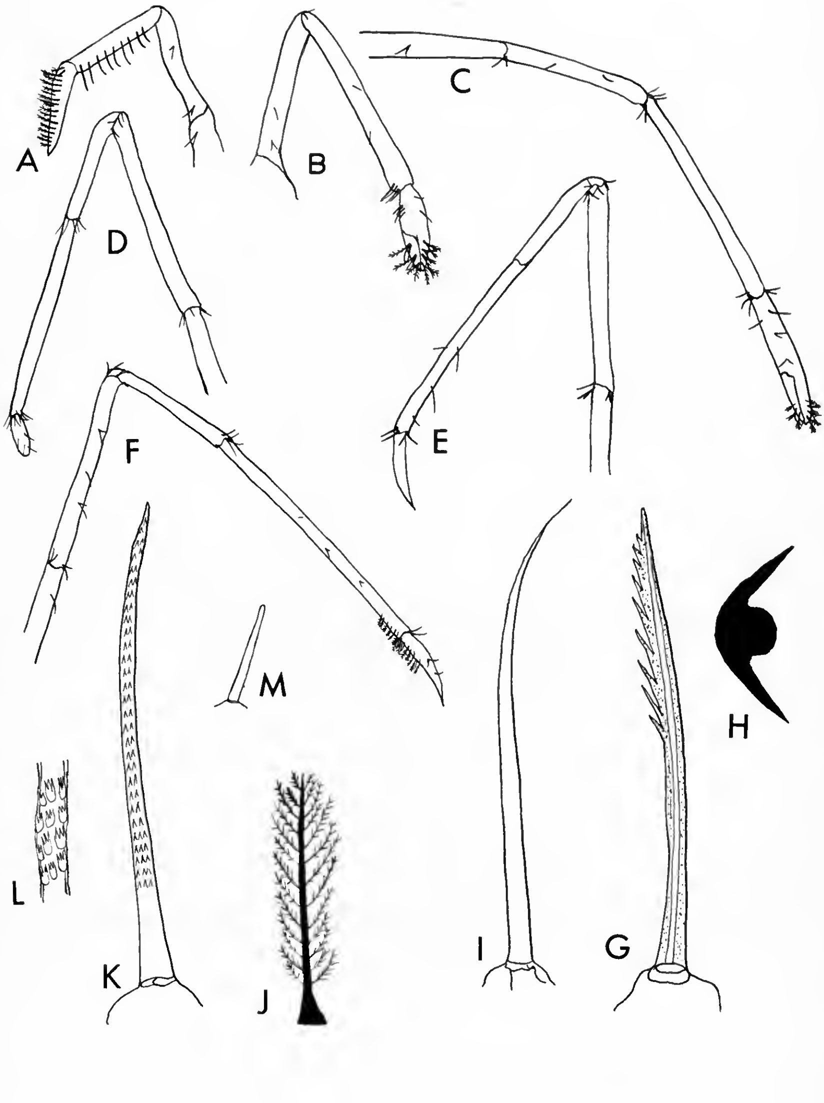

FIG. 1. **A**, Third maxilliped; **B**, First pereiopod; **C**, Second pereiopod; **D**, Third pereiopod; **E**, Fourth pereiopod; **F**, Fifth pereiopod; **G**, Serrate seta; **H**, Cross-section of serrate seta showing angle orientation of subsetules to shaft; **I**, Simple seta; **J**, Plumose seta; **K**, multi-denticulate seta; **L**, Close-up of multi-denticulate seta showing brush-like nature of subsetules; **M**, Squat-hair seta.

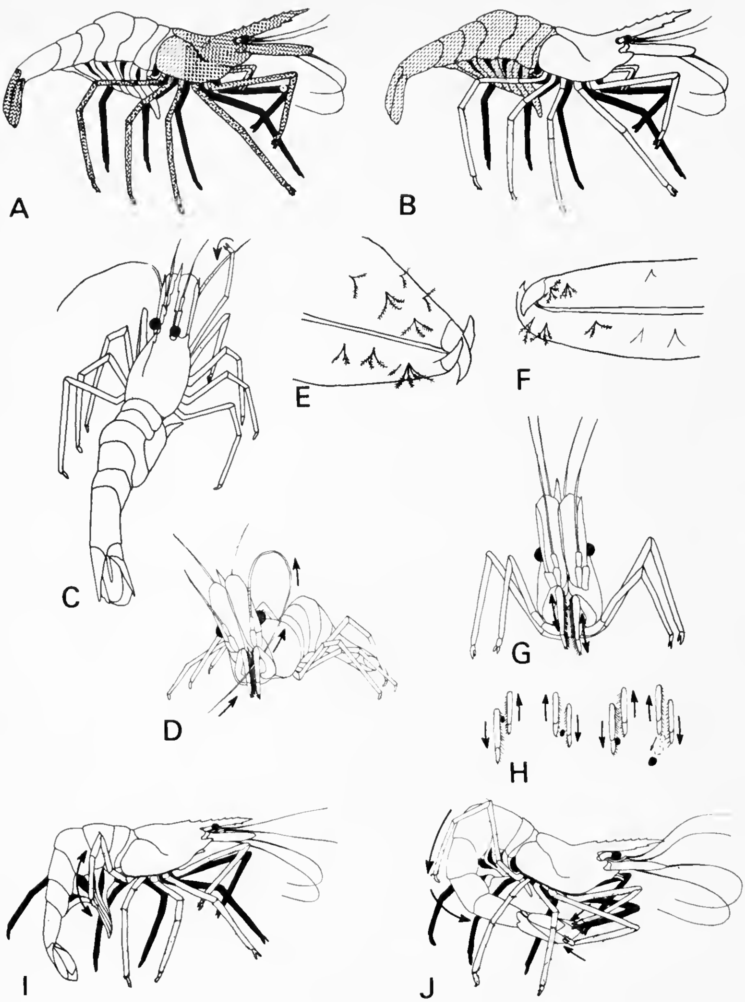

FIG. 2. **A**, Double-hatched area defines the field of operation of first and second pereiopod, single-hatched area indicates the field of operation of second pereiopod only; **B**, Hatched area field of operation of fifth pereiopod; **C**, Grooming of second antenna in carpus-propodus joint of first pereiopod; **D**, Grooming of second antenna by the third maxillipeds, arrows indicate direction in which flagellum is pulled; **E**, Tongue and groove locking mechanism of second pereiopod of *Pandalus danae;* **F**, Locking mechanism of second pereiopod of *Palaemonetes kadiakensis;* **G**, Auto-grooming of third maxillipeds, arrows indicating movement of appendages; **H**, Diagrammatic view of sequential stages in auto-grooming of third maxillipeds; **I**, Grooming of pleopods, arrow indicating motion of fifth pereiopod; **J**, Grooming of abdomen and telson, large arrows indicate movement of fifth pereiopod, small arrows indicate movement of first and second pereiopod chelae.

setae for this purpose (fig. 2a,b). The pereiopods also groom independently of each other and frequently reached across to preen opposite sides of the individual.

Several distinct types of setae are found on the grooming appendages (fig. 1g-m): serrate, simple, plumose, multi-denticulate, and squat-hairs.

Third Maxillipeds

The third maxilliped, composed of four segments, are larger than the other maxillipeds and have dense patches of serrate setae medially on the fused propodus and dactylus (pl. I, fig. 1). The setules lining the setal shaft occur at 45^0 angles to each other (fig. 1h), and are restricted to the distal two-thirds of the setal shaft.

The third maxillipeds groom the first and second pereiopods and the antennae. The chelae of the first and second pereiopods are groomed as a result of numerous passes through the third maxillipeds which are held horizontal to the substrate. After these pereiopods are groomed, the third maxillipeds remove debris and epizoites by the mutual rubbing of each other (fig. 2g). The maxillipeds rub vertically against each other's setae causing the lodged debris to drop to the substrate (fig. 2h), an activity also noted by Bauer (1975) in *Pandalus.*

The first antennae are also groomed by the third maxillipeds in the following manner: the first antennae are lowered toward the third maxillipeds; the maxillipeds raise themselves slightly, and clasp the base of the antennae; the first antennae are then drawn through the setation of the third maxillipeds as the antennae resume the normal horizontal resting position. This grooming occurs frequently and is usually coupled with cleaning of the second antennae, which will be discussed below.

First pereiopods

The first pereiopods of *Palaemonetes kadiakensis* have locomotory, feeding, and grooming functions. As in most caridean prawns, the first pereiopod is chelate and is composed of seven segments. The chelae are used to delicately probe the substrate for food and tear bits of material apart with the aid of the third maxillipeds.

The propodus and dactylus of the chelae are armed with three types of setae: serrate, multi-denticulate, and squat-hairs (pl. I, fig. 3), serving various grooming functions.

The dactylus and distal half of the propodus are armed with long multi-denticulate setae (pl. I, fig. 4), composed of toothed setules

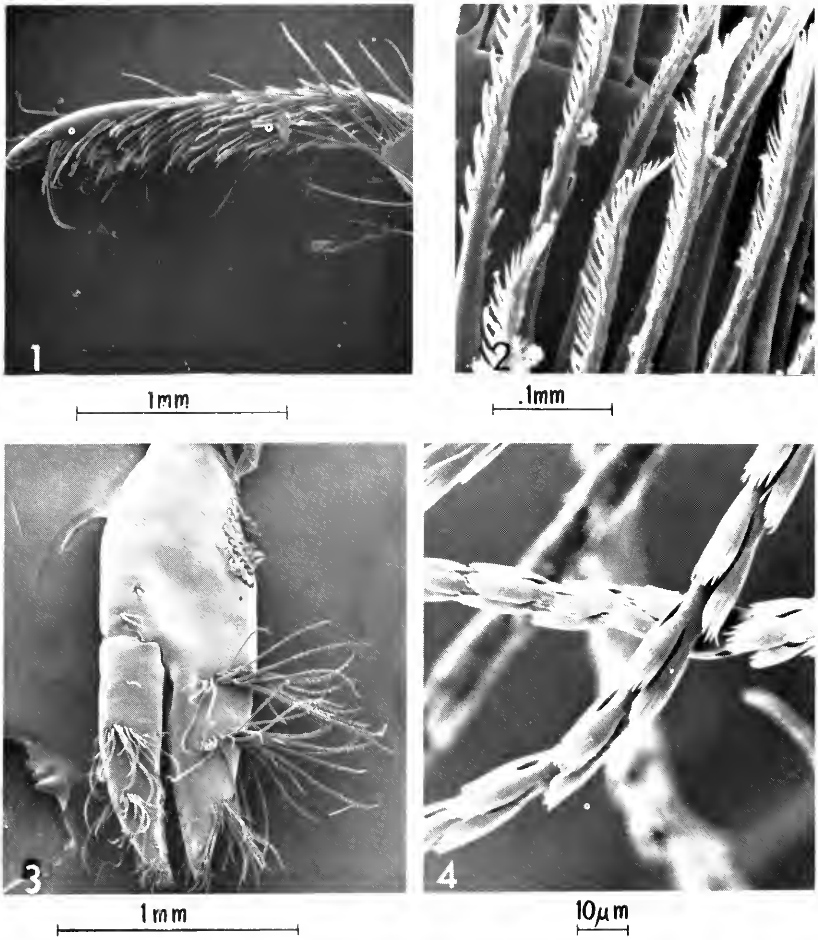

PLATE I. **1**, Third maxilliped; **2**, Close-up of serrate setae on third maxilliped; **3**, Chela of first pereiopod; **4**, Close-up of subsetules of multi-denticulate seta on first pereiopod.

along each setal shaft. Each setule has individual subsetules which give it a comb-like appearance (pl. II, fig. 1). The inner medial surfaces of the propodus and dactylus are armed with short, evenly spaced setae. These setae are termed squat-hairs. The squat-hairs located medially on the inner surface of the propodus and dactylus are apparent under light and SEM photography (pl. II, fig. 2), and are thought to be advantageous in gripping, scraping, and abrading (Bauer, 1975). Shelton & Laverack (1970) suggested that this type of setation may also be chemoreceptive.

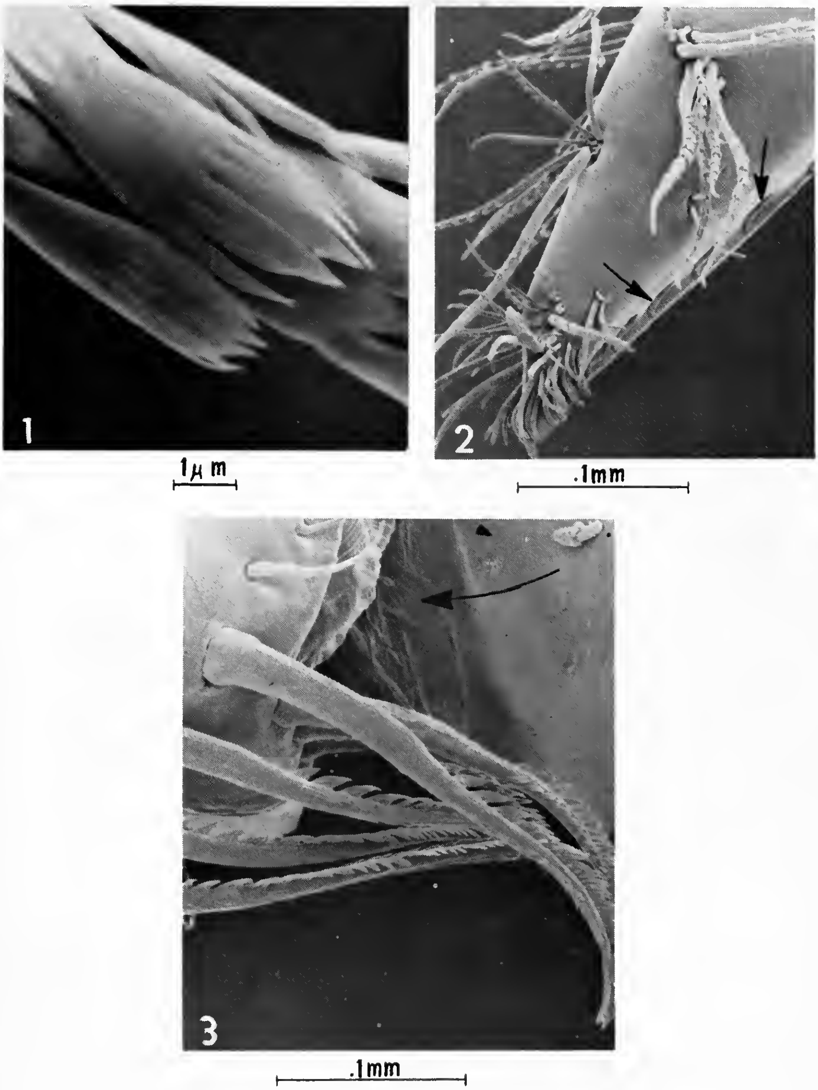

PLATE II. 1, Close-up of subsetules of multi-denticulate seta; 2, Terminus of first pereiopod with arrows indicating a row of squat-hair setae; 3, Carpus-propodus joint of first pereiopod, with arrow indicating position of antennular flagella in grooming.

The third setal type seen on the first pereiopods is serrate, found densely packed in the joint between the carpus and propodus (pl. II, fig. 3). This serrate setal type has rows of teeth laterally along the shaft and serrations that are not opposite on the shaft, but usually within 45-120° of each other (fig. 1g,h). The serrate setae have also been suggested to be chemoreceptive (Farmer, 1974). The proximal portion of the propodus is lined with rows of stiff, short, serrate setae which are individually set into sockets. The brush-like nature of this setation is presented by SEM stereo pairs (pl. III, fig. 1a,b). These serrate setae on the carpus are longer and denser than the more uniformly spaced serrate setae on the propodus (pl. III, fig. 3). Serrate setae are brush-like in appearance and their dense nature forms a network of combs which provide a surface area for grooming the antennae when the joint is flexed.

The first pereiopods groom primarily cephalic structures (fig. 2a), and also parts of the telson. The chelae pick and preen at the crevices of the exoskeleton, vigorously pulling and digging at the arthrodial membranes. The chelae open and close rapidly while passing across the carapace and rostrum during grooming periods. The squat-hairs, located medially on the inner surface of the propodus and dactylus, may act as scraping devices during the rapid movement of the chelae over the exoskeleton. These serrate setal bundles on the distal end of both the propodus and dactylus are used as brushes to clean the gill lamellae and the lining of the branchial chamber.

The telson is simultaneously groomed by the first and second pereiopods. The prawn is supported by the third and fourth pereiopods as the telson is then brought anteriad and ventrad under the carapace. The first and second pereiopods pick at the uropods and the chelae rapidly open and close while passing across the surface of the telson (fig. 2j). The pereiopods of *Palaemonetes kadiakensis* are quite flexible at the joints, enhancing their grooming efficiency.

The second antenna of the prawn is groomed with greater frequency than any other part of the prawn. The second antenna is brought anterior as the carpus-propodus joint of the first pereiopod hooks onto the base of the second antennular flagellum (fig. 2c). Each antenna is then pulled ventrad by the first pereiopod toward the third maxillipeds. In the process of lowering the antennular flagellum the carpal-propodal joint slides down the length of the antenna. The third maxillipeds then clasp the base of the flagellum, where-

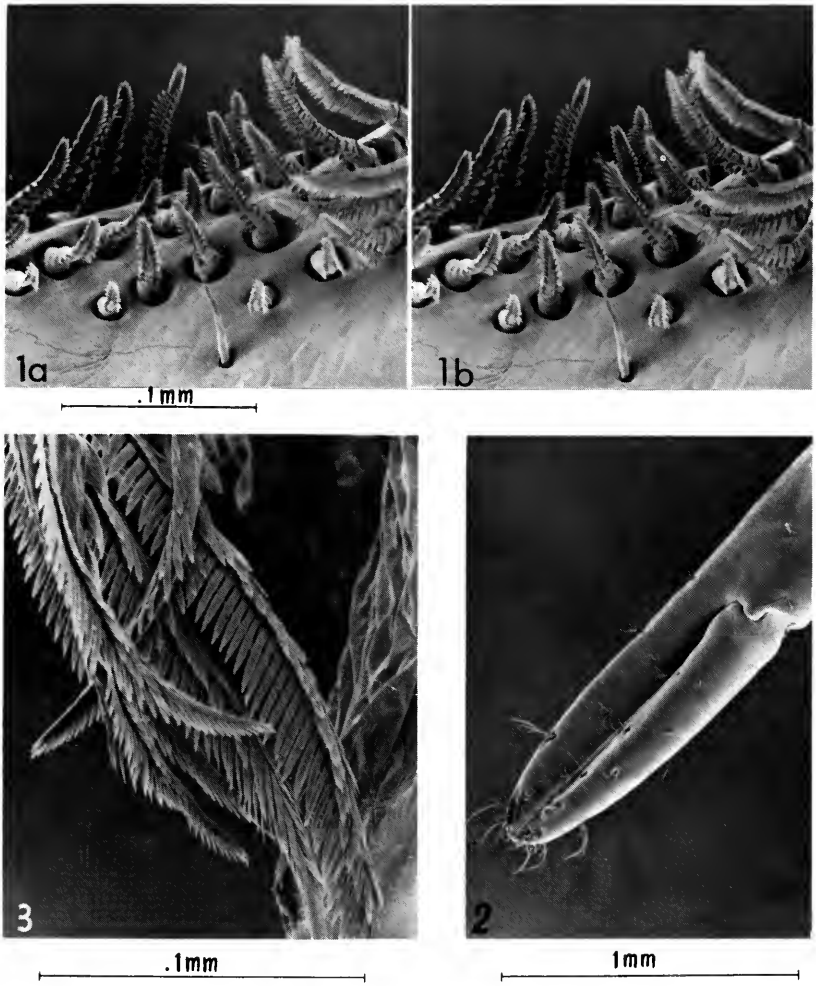

PLATE III. 1a, b, Stereo SEM of serrate setae on proximal third of propodus of first pereiopod; 2, Second pereiopod; 3, Close-up of serrate setae in carpus-propodus joint of first pereiopod.

upon the antenna is pulled through stiff grooming brushes of the third maxillipeds as it resumes its normal horizontal position (fig. 2d). Following this antennular grooming, the third maxillipeds also autogroom. The antennular flagella are actually double-groomed by this elaborate process. The carpus-propodus joint of the first pereiopod is heavily armed with dense serrate setae, which, when flexed around the antennae, form a network of brushes that encloses the entire flagellum as it moves through the joint (pl. II, fig. 3).

The first pereiopod setal groups are cleaned by rubbing the distal portion of the leg through the stiff serrate setae of the third maxillipeds. Following this action, the chelae are often autogroomed by brushing against each other for short periods, thus removing any additional debris from the serrate setae.

Second pereiopods

The second pereiopods behave in a manner similar to the first pereiopods. The chelae of the second pereiopods are more slender and pointed than those of the first pereiopods (pl. III, fig. 2). The distal portion of the chela is armed with multi-denticulate setae set into deep sockets with many setae per socket (pl. IV, fig. 1a,b). There is sparse multi-denticulate setation of the distal end of the propodus and dactylus (pl. III, fig. 3). There are no setal groups on the carpus of the second pereiopod, as is seen on that of the first pereiopod, but as in the first pereiopod the second also has squat-hairs lining the medial surface of the propodus and dactylus.

The second pereiopod has a locking mechanism on the tip of the chela. The propodus and dactylus have large terminal tooth-bearing movable setae that fit together tightly when the chela is closed (pl. IV, fig. 3). Bauer (1975) observed that the second pereiopod of *Pandalus danae* had a tongue and groove locking mechanism (fig. 2e). *Palaemonetes kadiakensis* has a locking mechanism on both the first and second pereiopods which lock much like the clasps on a purse. (fig. 2f).

The second pereiopods supplement the first pereiopods in grooming the cephalic regions and have virtually the same field of activity. The second pereiopods, however, do not groom the antennae nor much of the rostral area, and they reach farther posterior on the carapace (fig. 2a). The second pereiopods preen the edges of the branchiostegites and the peduncle of the eyestalks more than the first pereiopods do. Since the chelae of this second pereiopod are armed with setae of the multi-denticulate type, they also may have important chemoreceptive functions.

Third and fourth pereiopods

The third and fourth pereiopods are the principal walking appendages of the prawn and are long and pointed at the tip (fig. 1d,e).

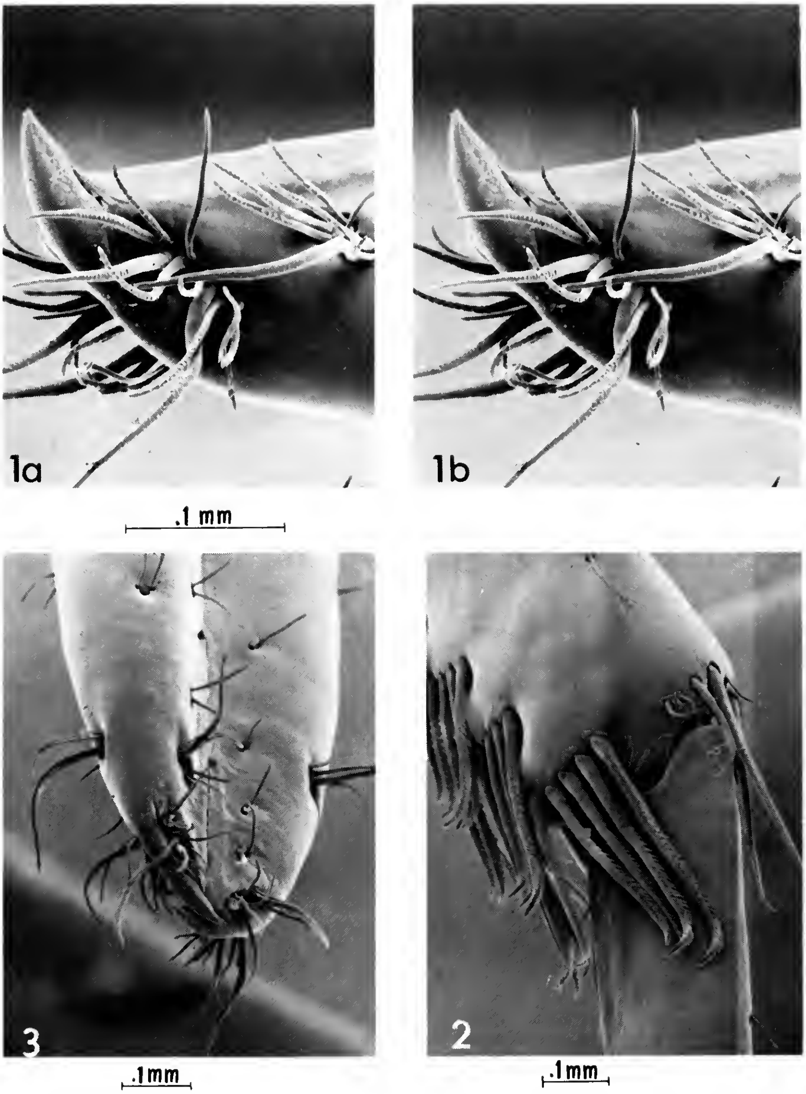

PLATE IV. 1a, b, Stereo SEM of lateral view of second pereiopod; 2, Carpus-propodus joint of fifth pereiopod; 3, Oblique view of second pereiopod chela showing interlocking terminal setae.

The setal structures of these pereiopods indicate that these appendages are not morphologically designed for grooming, as they are devoid of complex setation. Most of the setae are simple, with solitary shafts lacking the subsetules or serrations of the grooming pereiopods (fig. 1b,c,f).

The main functions of these two pereiopods during grooming periods are support and balance. Removal of the first, second, and fifth pereiopods does not impair locomotion and maneuverability.

Fifth pereiopods

The fifth pereiopods are the longest and most flexible of all the walking legs and groom the abdomen and tail fan of the animal. Serrate setae extend ventrally between the carpal-propodal joint (pl. IV, fig. 2).

The fifth pereiopods groom the dorsum of the abdomen. This is accomplished as the prawn shifts its weight forward on the third and fourth pereiopods as the telson is flexed forward, forming an inverted "U." The fifth pereiopod then runs its serrate setae dorsally down the entire length of the abdomen, beginning with the posterior edge of the carapace and ending at the tip of the telson (fig. 2j). The serrate setae on the fifth pereiopod are extremely dense and groom the entire dorsum of the abdomen (pl. V, fig. 1).

The prawn remains in this flexed position for extended periods of time as the fifth pereiopod repeatedly sweeps the abdominal region. This behavior is frequently coupled with the preening of the telson by the first and second pereiopods (fig. 2j).

The fifth pereiopods are important in the grooming of the abdomen in both prawns. Heavy bundles of serrate setae are seen in the carpal-propodal joint of both species. The behavioral patterns of cleaning the abdomen are somewhat different. *Palaemonetes kadiakensis* brings its abdomen beneath the carapace as the fifth pereiopods stroke the dorsum of the abdomen. Bauer also reported this behavior in *Pandalus*, but noted this species more typically groomed a straightened abdomen with brushing and scratching movements of the fifth pereiopods.

Grooming is an integral part of the activities of *Palaemonetes kadiakensis*. It is evident in this study that elaborate morphological and behavioral adaptations have been developed for the removal of fouling organisms and debris, and that a large proportion of time and energy is expended in the process of cleaning. The Infraorder Caridea has successfully radiated into marine, brackish, and fresh-

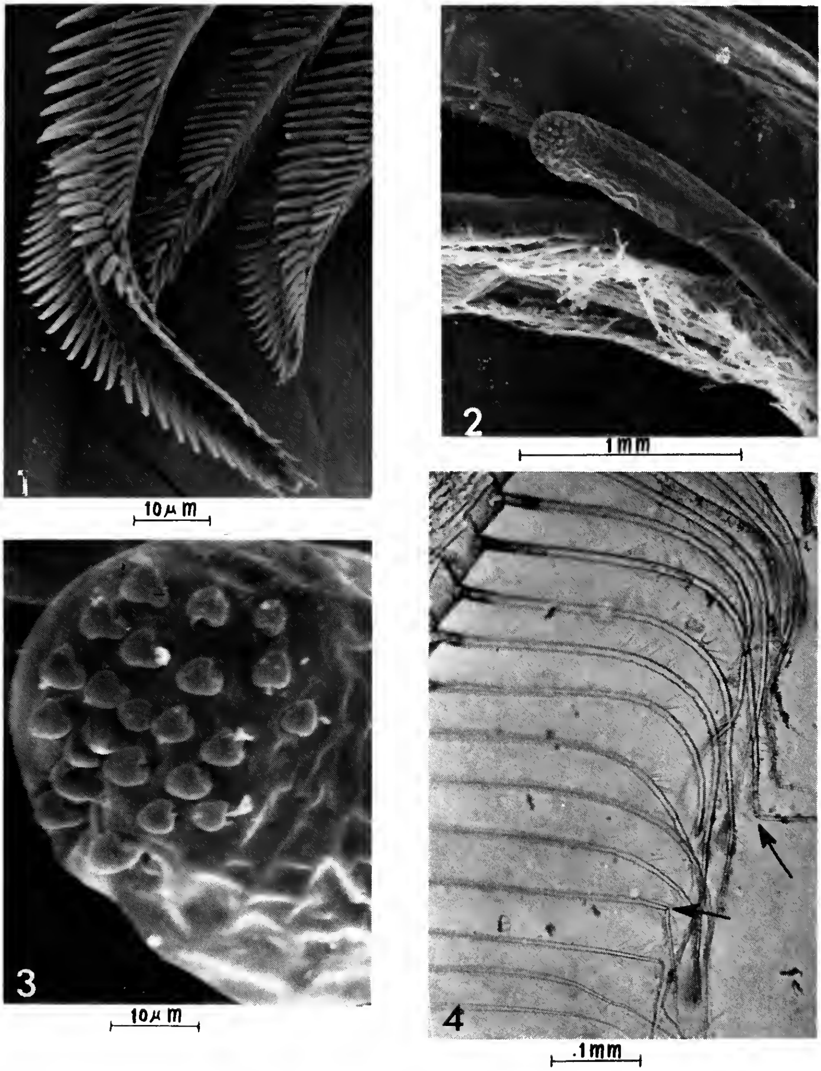

PLATE V. 1, Brush-like serrate setae on fifth pereiopod; 2, Appendix interna on pleopods; 3, Close-up of terminus of appendix interna showing the mushroom setae for interlocking with opposing appendix interna; 4, Light micrograph of plumose setae on pleopod, arrows indicating bent or broken setae.

water habitats. One factor that may have contributed to this success is the development of efficient grooming patterns.

Monitoring the external environment is vital to the success of any animal. The caridoid escape reaction of *Palaemonetes kadiakensis* is its primary defense mechanism against predators and it is probably largely triggered by sight, vibrations, or chemoreception. If sensory sites are fouled, information from the environment could be lost. Olfaction in *Palaemonetes kadiakensis* is accomplished at sites of aesthetascs (extensions of the exoskeleton). They are found on the base of the first antennae in *Palaemonetes kadiakensis.* The frequent and repeated groomings of the antennae keeps the aesthetascs free of fouling organisms and debris, allowing olfaction to be constant and accurate. Without regular grooming, vital information from the environment could be lost due to the inhibition of water currents through the rows of aesthetascs (Bauer, 1975). Chemoreception of the antennae, pereiopods, and maxillipeds aid in the securing of food, consequently fouling of such sites could hinder the receptivity and hence the locating of food sources (Barber, 1960; Shelton & Laverack, 1970). The third maxillipeds are heavily armed with serrate setae and are constantly accepting and rejecting possible food. The serrate setae of the first and second pereiopods also select and reject materials from the substrate. Clogging of these chemoreceptive setae may limit the prawn's ability to locate food. The eyestalks of *Palaemonetes kadiakensis* are constantly twitching and are groomed by the first and second pereiopods to discourage fouling.

In the genus *Palaemonetes*, males respond only to females which have recently molted to breeding condition. The recognition of attractiveness by the male occurs with contact of his antennae with any surface of the female; thus sex recognition would appear to be determined by a non-diffusible coating of the integument of the female (Burkenroad, 1947). The mating stimulus initiating the palaemonid mating behavior suggests that recognition of a receptive female by the male has an important visual component (Nouvel & Nouvel, 1937; Hoglund, 1943). Regardless of which interpretation of palaemonid sex recognition is correct, be it visual or chemical, if sensory sites are fouled, mating would be hindered.

The caridean respiratory and feeding current is an anteriad stream of water drawn under the posterior and lateral edges of the carapace and discharged anteriorly on either side of the mouth. This important flow would be interrupted by debris and epibionts which aggregate along the edges of the branchiostegites if they were not removed in some manner.

Setation plays an important role in locomotion in *Palaemonetes kadiakensis.* Swimming is accomplished in this prawn by the appendix interna locking the pairs of pleopods. The tips of these structures, which are found on all but the first pleopods, hold the elements together while the prawn is swimming (pl. V, fig. 2). The appendix interna is armed with mushroom-shaped setae which serve to hook the pleopods together (pl. V, fig. 3). The plumed setae, which have smooth shafts inserted into sockets and have numerous setules, are located on the pleopod margins (fig. 1j). These setae extend the surface area of the pleopod and form "paddles" which propel the prawn through the water. If these setae were not groomed regularly, they would soon become fouled and eventually break, causing the resistance between the water and the pleopods to be weakened, thus hindering locomotion (pl. V, fig. 4).

Molting is one of the most important aspects of crustacean physiology. The normal physiology of prawns is continuously concerned with the successive stages of the molt cycle. Between molts, *Palaemonetes kadiakensis* keeps its integument free of fouling organisms and debris by grooming. Whereas ecdysis frees the crustacean body of its old cuticle and any fouling debris, it can be interrupted periodically by hibernation, ovarian maturation, and carrying of developing eggs (Passano, 1960). It is during these intermittent periods that grooming is extremely important.

Temperature influences molting (Passano, 1960). Crustaceans exhibit increased molting activity during periods of higher temperatures and significantly reduced activity (anecdysis) during times of low temperatures (Hiatt, 1948; Balesdent-Marquet, 1955). *Palaemonetes kadiakensis* is subjected to low temperatures for two to five months of the year. During this time, molting seems to cease and grooming is needed to remove fouling organisms and debris until the molt cycle resumes in warmer weather.

An effective grooming mechanism in these crustaceans is essential. Such elaborate grooming mechanisms have undoubtedly played a role in the relative success of the carideans as natant decapods.

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