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GROOMING BEHAVIOR AND MORPHOLOGY IN THE DECAPOD CRUSTACEA

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ABSTRACT

Many decapod crustacean species have specialized structures for grooming the body to keep it free of epizoic growth and particulate fouling. Among the decapod species examined, preening of the chemosensory antennules with the third maxillipeds was the most widespread and morphologically conservative behavior. Penaeidean, caridean, and stenopodidean shrimps possess characteristic setal brushes on the first cheliped for cleaning the chemotactile antennular flagella. Reptant species use only the third maxillipeds for grooming these flagella. Gill cleaning mechanisms vary widely: cheliped brushes, setae arising from thoracic setobranchs, setiferous thoracic epipods.

Decapods use chelipeds and setal brushes at the tips of walking legs for grooming general body surfaces. This behavior is common in the Natantia (*s.l.*) but is poorly developed in the Brachyura. I hypothesize that epizoic growth interferes with swimming in shrimps, and it must be removed by preening. In the ambulatory Brachyura, selection pressure to remove epizoic growth may be less intense. Many decapod species that do not appear to have general body grooming specializations are nonetheless clean. A variety of mechanisms besides grooming may serve as antifouling adaptations in these species.

Grooming structures have been little studied, but they may have considerable systematic value in the study of decapod phylogeny.

Many decapod crustacean species spend considerable time engaged in grooming or cleaning. These species have a variety of structures and behaviors that function to prevent body fouling by epizoites and particulate debris. During grooming, the decapod scrapes its exoskeleton with brushes of serrate and multidenticulate setae. Vital sensory and respiratory structures, such as antennules, antennae, and gills, are the most frequently groomed. In some species, there are prolonged bouts of preening in which the carapace and abdomen are carefully brushed and scrubbed. The cleaning of brooded embryos by females is an important grooming behavior in many decapod species.

The functional morphology and biological role of grooming in caridean shrimps has been studied by Bauer (1975; 1977; 1978; 1979). In experiments, amputation of cleaning limbs resulted in fouling of the body and its remaining appendages. Shrimps prevented from grooming the antennules suffered severe fouling and sometimes loss of olfactory hairs (Bauer, 1975; 1977). Ungroomed gills became fouled and clogged, and brooded embryos not cleaned by females suffered significant mortality (Bauer, 1979). General body surfaces, if not regularly cleaned, served as substrates for the growth of fouling organisms (Bauer, 1975; 1978). Felgenhauer and Schram (1978) also found higher rates of fouling on the freshwater shrimp *Palaemonetes kadiakensis* when grooming limbs were amputated.

The few experimental studies on other decapods also suggest the importance of grooming behavior. Snow (1973) found that hermit crabs prevented from grooming developed heavy antennular fouling. Porcellanid crabs showed severe gill fouling and susceptibility to infection by larvae of a rhizocephalan parasite after ablation of the grooming chelipeds (Larry Ritchie, personai communication). Walker (1974) showed that maxillipedal epipods, which clean the gills in brachyuran crabs, helped reduce infestation by gill barnacles in the blue crab *Callinectes sapidus*.

Outside of the recent studies on caridean shrimps cited above, there has been little work on the identification and description of grooming structures and behaviors in the Decapoda. The purpose of this report is to describe decapod cleaning structures and behaviors and to give the distribution of grooming characters in decapod species I have examined. I discuss the possible relationship between the level of general body grooming specialization and morphological-locomotory trends within the Decapoda. I offer possible explanations for the apparent absence of grooming structures in certain decapod groups.

METHODS

Table 1 presents grooming mechanisms in non-caridean species of decapod crustaceans that I have examined. I gathered these data by observing live animals (primarily in aquaria but also in the field), by examining preserved specimens, and by searching the literature for previously reported observations. With living animals, any repeated rubbing, scraping, picking, or combing actions by appendages directed towards other appendages or parts of the decapod's body were considered grooming behaviors. (I exclude the interaction among mouthparts from this definition.) Experimental studies on caridean shrimp (Bauer, 1975; 1977; 1978; 1979) and on the porcellanid crab *Petrolisthes cabrilloi* (Larry Ritchie, personal communication) have verified that such behaviors do clean the bodies of these decapods. In this study, when I inferred grooming function of a structure solely from the morphology of a preserved specimen, I used the criterion that the structure was similar to a homologous one that has been directly observed in cleaning in another decapod species. Thus far, this method has been accurate. In several species, I have confirmed the grooming function of a setal brush or a cheliped, initially inferred on a morphological basis, when living representatives of those species became available for observation. Distribution of grooming characters in caridean species discussed in this report is given in Bauer (1977; 1978; 1979).

RESULTS

Antennular Grooming

Antennular preening by the third maxillipeds is the most widespread and conservative of decapod cleaning behaviors. It is present in most of the decapod species I observed (Table 1; Bauer, 1977). In antennular cleaning, the endopods of the third maxillipeds reach up to grasp an antennule which has been lowered between them (Fig. 1). Both the inner flagellum and the outer flagellum (which carries the olfactory esthetascs) are drawn through rows of serrate setae on the maxillipedal endopods as, simultaneously, the antennule is raised back up to the normal upright position and the maxillipeds are lowered. After a bout of antennular preening, the decapod often rubs the endopods of the third maxillipeds together to rid the endopodal setae of accumulated debris.

Preening of the Antennal Flagellum

Most caridean shrimp clean the long chemotactile antennal flagella with setal brushes on the first pair of chelipeds. The cleaning brushes are located on opposite sides of the carpal-propodal joint (Bauer, 1975; 1978). During cleaning, the base of an antennal flagellum is first caught between these brushes. The flagellum is then drawn through the brushes, and it is scraped by their serrate setae (Fig. 4, Bauer, 1978). In all species observed, the antennal flagellum was simultaneously drawn through the third maxilliped's cleaning setae to varying degrees. For example, in *Pandalus danae* Stimpson the third maxillipeds were highly involved; in contrast, the third maxillipeds played little part in the antennal cleaning of *Palaemon ritteri* Holmes. However, there were no antennal cleaning brushes observed in alpheid and atyid carideans: these shrimps groom the antennal flagella with only the third maxillipeds.

Penaeidean and stenopodidean shrimp that have been examined (Table 1) clean

Table 1. Grooming mechanisms of decapod crustacean species (for caridean species, see Bauer, 1977; 1978; 1979); P, present; A, absent.

Species	(1) Antennular grooming by the third maxillipeds	(2) Antennal flagellum groomed with the carpal-propodal brush of pereopod 1	(3) Gill cleaning	(4) General body grooming by anterior chelipeds	(5) General body grooming by posterior pereopods	Source of Information: D, direct behavioral observation by the author; M, inferred from morphology; L, from the literature; numbers refer to column headings
Section Penaeidea						
Penaeidae						
Penaeus brevirostris Kingsley	P	P	Compound setae on thoracic epipods	Chelipeds 1–3	A (no setal brushes)	1:M; 2:D; 3–5:M
P. merguiensis De Man	P	P	Compound setae on thoracic epipods	Chelipeds 1–3	A (no setal brushes)	1, 2, 4, 5:L (Hindley and Alexander, 1978; J. P. R. Hindley, pers. comm.) 3, 5:M
Aristaeidae						
Gennadas incertus Balss	P	P	? (epipods reduced, setae lacking)	Chelipeds 1–3	A (no setal brushes)	1–5:M; 4:D on *Gennadas* sp.
Section Stenopodidea						
Stenopodidae						
Stenopus hispidus (Olivier)	P	P	Chelipeds 1 and 2	Chelipeds 1 and 2	A (no setal brushes)	1:M, D; 2–4, M, D, L (Stolen, 1964); 5:D, M
S. scutellatus Rankin	P	P	Chelipeds 1 and 2	Chelipeds 1 and 2	A (no setal brushes)	1–5: Joseph Goy (pers. comm.)
Microprosthema semilaeve (von Martens)	P	P	Chelipeds 1 and 2	Chelipeds 1 and 2	A (no setal brushes)	1–5: Joseph Goy (pers. comm.)

Table 1. Continued.

Species	(1) Antennular grooming by the third maxillipeds	(2) Antennal flagellum groomed with the carpal-propodal brush of pereopod 1	(3) Gill cleaning	(4) General body grooming by anterior chelipeds	(5) General body grooming by posterior pereopods	Source of Information: D, direct behavioral observation by the author; M, inferred from morphology; L, from the literature; numbers refer to column headings
Section Macrura						
Astacidae						
Procambarus clarkii (Girard)	P	A	Setobranch setae	Chelipeds 2 and 3	Brushes of serrate setae on pereopods 4 and 5	1–5:M; 1–2:D
Austropotamobius pallipes (Lereboullet)	P	A	Setobranch setae	Chelipeds 2 and 3	Brushes of serrate setae on pereopods 4 and 5	1–5:L (Thomas, 1970)
Nephropidae						
Nephrops norvegicus (L.)	P	A	Setose thoracic epipods lying between gills	Chelipeds 2 and 3	Brushes of serrate setae on pereopods 4 and 5	1, 2, 4, 5:L (Farmer, 1974) 3:M
Homarus americanus (H. Milne-Edwards)	P	A	Setose thoracic epipods lying between gills	Chelipeds 2 and 3	Brushes of serrate setae on pereopods 4 and 5	1:D, 1–5:M
Palinuridae						
Panulirus interruptus (Randall)	P	A	Setose thoracic epipods lying between gills	Brushes of serrate setae on achelate pereopods 1, 2, 3	Brushes of serrate setae on pereopods 4 and 5	1–5:M; 4, 5:D

Table 1. Continued.

Species	(1) Antennular grooming by the third maxillipeds	(2) Antennal flagellum groomed with the carpal-propodal brush of pereopod 1	(3) Gill cleaning	(4) General body grooming by anterior chelipeds	(5) General body grooming by posterior pereopods	Source of Information: D, direct behavioral observation by the author; M, inferred from morphology; L, from the literature; numbers refer to column headings
Section Anomura						
Axiidae						
Calocaris quinqueseriatus (Rathbun)	P	A	Setobranch setae	P (?); chelipeds 2	Pereopods 4 and 5 with propodal brushes of serrate setae	1–5:M
Axius vivesi Bouvier	P	A	Setobranch setae	P (?); chelipeds 2	Pereopods 4 and 5 with propodal brushes of serrate setae	1–5:M
Callianassidae						
Callianassa californiensis Dana	P	A	Chelate 5th pereopods	P (?); chelipeds 2	Pereopods 4 and 5	1–2:M; 3:M, D, L (MacGinitie, 1934); 4:M; 5:M, D, L
Galatheidae						
Pleuroncodes planipes Stimpson	P	A	Chelate 5th pereopods	Chelipeds 1	Chelate 5th pereopods	1, 2, 3, 5:M, D; 4:D
Porcellanidae						
Petrolisthes cabrilloi Glassell	P	A	Chelate 5th pereopods	A	Chelate 5th pereopods	1–5:M, D
Paguridae						
Paguristes turgidus (Stimpson)	P	A	Chelate 5th pereopods	A (?)	Chelate 5th pereopods	1–2:M, D; 3–5:M
Dardanus deformis (H. Milne-Edwards)	P	A	Chelate 5th pereopods	A (?)	Chelate 5th pereopods	1:M, L (Fig. 1); 2–5:M

Table 1. Continued.

Species	(1) Antennular grooming by the third maxillipeds	(2) Antennal flagellum groomed with the carpal-propodal brush of pereopod 1	(3) Gill cleaning	(4) General body grooming by anterior chelipeds	(5) General body grooming by posterior pereopods	Source of Information: D, direct behavioral observation by the author; M, inferred from morphology; L, from the literature; numbers refer to column headings
Lithodidae						
Lopholithodes foraminatus Stimpson	P	A	Chelate 5th pereopods	A (?)	Chelate 5th pereopods	1–5:M
Hippidae						
Emerita analoga Stimpson	A (cleaned by setal group on antenna 2)	A	Chelate 5th pereopods	A (?)	Chelate 5th pereopods	1–2:M, L (Efford, 1966, 1971); 3–5:M
Section Brachyura						
Homolidae						
Homola faxoni (Schmitt)	P	A	Setiferous epipods on maxillipeds 1–3 and pereopods 1–3	A (?)	A (?) (no setal brushes)	1–5:M
Dromiidae						
Dromidia larraburei (Rathbun)	P	A	Setiferous epipods on maxillipeds 1–3; also, tufts of setae arising from the body wall beneath the gills	A (?)	A (?) (no setal brushes)	1–5:M

Table 1. Continued.

Species	(1) Antennular grooming by the third maxillipeds	(2) Antennal flagellum groomed with the carpal-propodal brush of pereopod 1	(3) Gill cleaning	(4) General body grooming by anterior chelipeds	(5) General body grooming by posterior pereopods	Source of Information: D, direct behavioral observation by the author; M, inferred from morphology; L, from the literature; numbers refer to column headings
Raninidae						
Ranilia augustata Stimpson	P	A	Setiferous epipods on maxillipeds 1–3	A (?)	A (?) (no setal brushes)	1–5:M
Calappidae						
Hepatus kossmanni Neuman	P	A	Setiferous epipods on maxillipeds 1–3	A (?)	A (?) (no setal brushes)	1–5:M
Grapsidae						
Pachygrapus crassipes Randall	P	A	Setiferous epipods on maxillipeds 1–3	A (?)	A (?) (no setal brushes)	1, 2, 4, 5:M, D; 3:M
Majidae						
Libinia mexicana (Rathbun)	P	A	Setiferous epipods on maxillipeds 1–3	A (?)	A (?) (no setal brushes)	1–5:M
Loxorhynchus grandis Stimpson	P	A	Setiferous epipods on maxillipeds 1–3	P (?) chelipeds	P (?) last pereopod	1, 2, 4, 5:D, M; 3:M
Portunidae						
Callinectes sapidus Rathbun	P	A	Setiferous epipods on maxillipeds 1–3	P (chelipeds)	P (last pereopod)	1, 2, 4, 5:M, L (Pearson and Olla, 1977); 3:M, L (Walker, 1974)

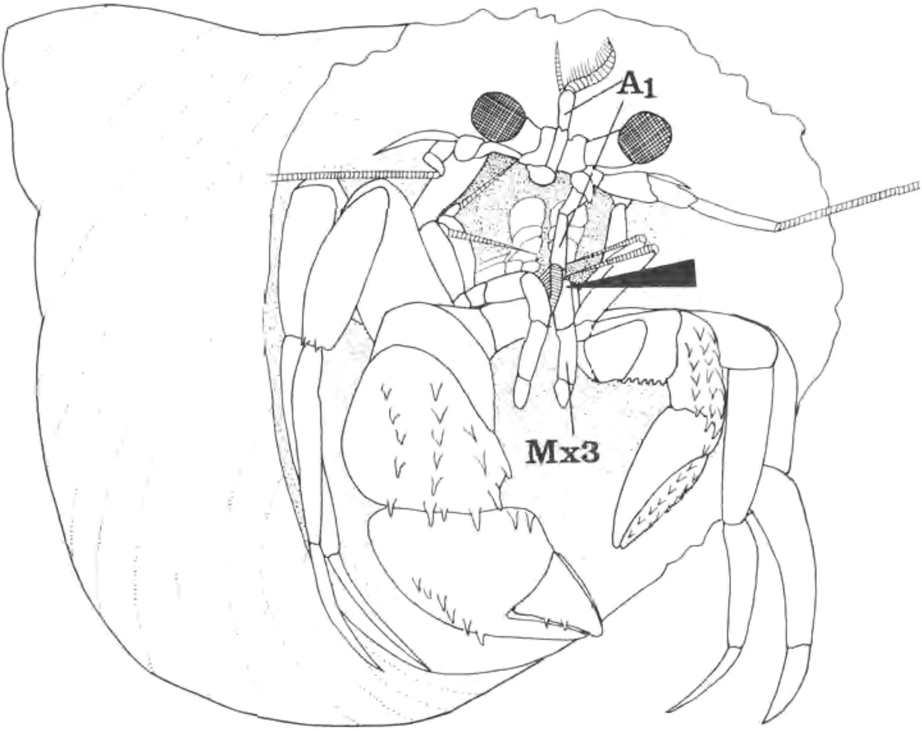

Fig. 1. Antennular preening in the hermit crab *Dardanus deformis* (adapted from a photograph by Ron and Valerie Taylor). A1, antennule; Mx3, third maxilliped; arrow shows an antennule being preened.

the antennal flagella with setal brushes that are very similar to those of carideans in setal composition, location, and function. The antennal cleaning brushes of *Penaeus brevirostris* (Fig. 2) are typical of those I have observed in natantians. One group of serrate setae on the carpus curves towards the carpal-propodal joint; these appear to hold the antennal flagellum in place as it is drawn through the brushes. Both the carpal and propodal brushes are composed of serrate setae for scraping the flagellum as it slides through the brushes.

The antennal flagellar cleaning brushes of pereopod 1 are present in many penaeidean species. Anderson and Linder (1943), in their key to American penaeids, used presence of the propodal brush (function unstated) in the then recognized Penaeinae, Solenocerinae, and Aristaeinae to distinguish these groups from the Eusicyoninae. Hansen (1919) illustrated these setal brushes for the sergestid *Sergestes orientalis* (Hansen). Judkins (1978) also figured the carpal and propodal brushes for *Sergestes geminus* (in his Fig. 2m) and used their presence as a character in the diagnosis of the *S. edwardsii* species group (8 species).

In contrast to the Natantia, no reptant species examined showed antennal cleaning brushes on the first chelipeds. All reptant species I observed groomed the antennal flagella with the third maxilliped using movements much like those of antennular preening.

Gill Cleaning Mechanisms

Enclosure of gills inside a branchial chamber is a characteristic feature of decapod crustaceans. Gills are protected within a narrow space through which res-

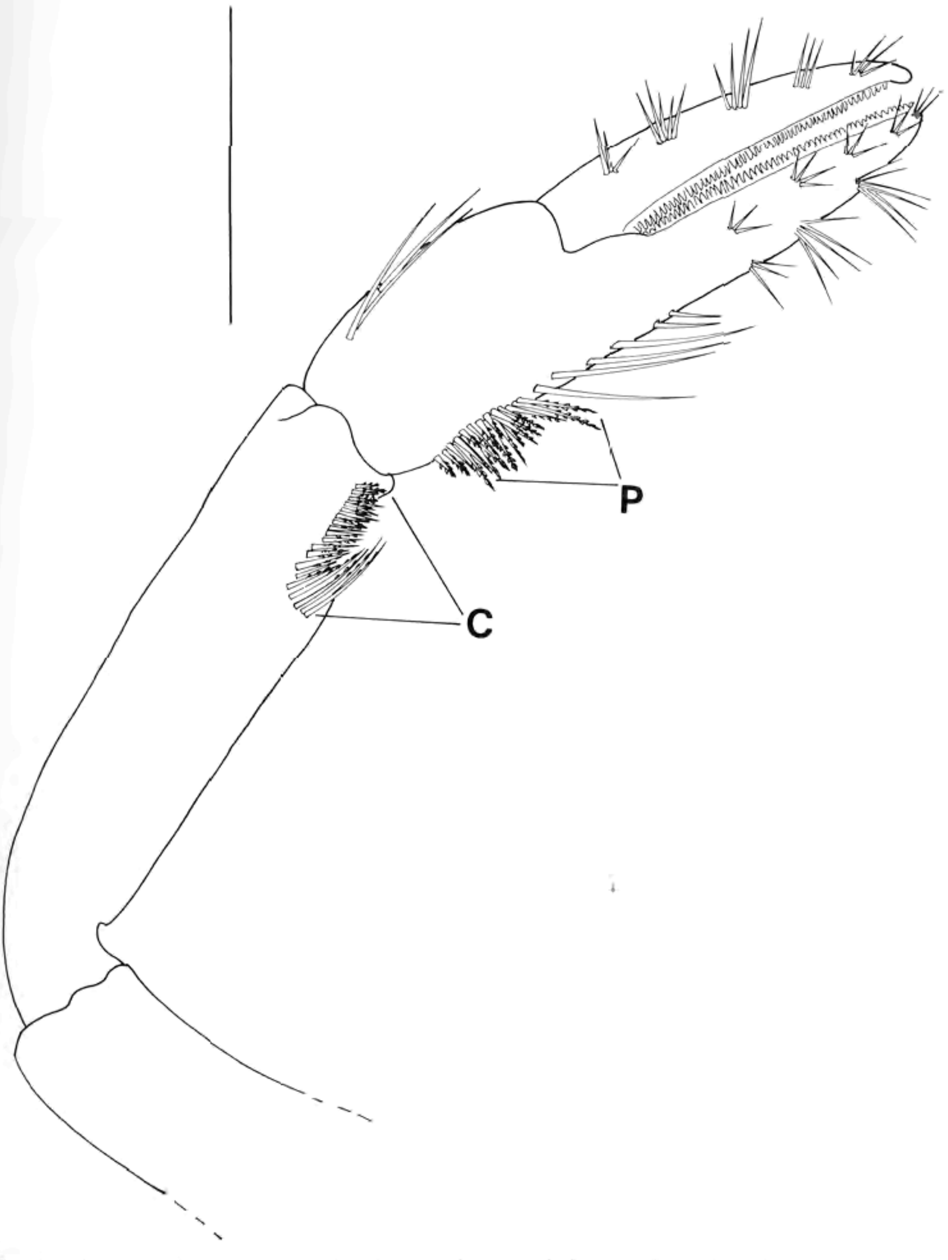

Fig. 2. Antennal flagella cleaning brushes on the first cheliped (left, medial view) of the penaeid shrimp *Penaeus brevirostris*. C, carpal setal brush; P, propodal setal brush; scale, 2.0 mm; additional setae on the carpus omitted for clarity.

piratory water can be efficiently pumped. But gill confinement has a disadvantage: the numerous gill filaments, rami, or lamellae create a sediment trap which filters fine particles carried in by the respiratory current. Many decapod species have setal filters guarding the inhalant openings to the gill chamber. However, very fine filtering of the respiratory stream is not possible because it would impede current flow. As a result, a number of gill cleaning mechanisms have evolved in

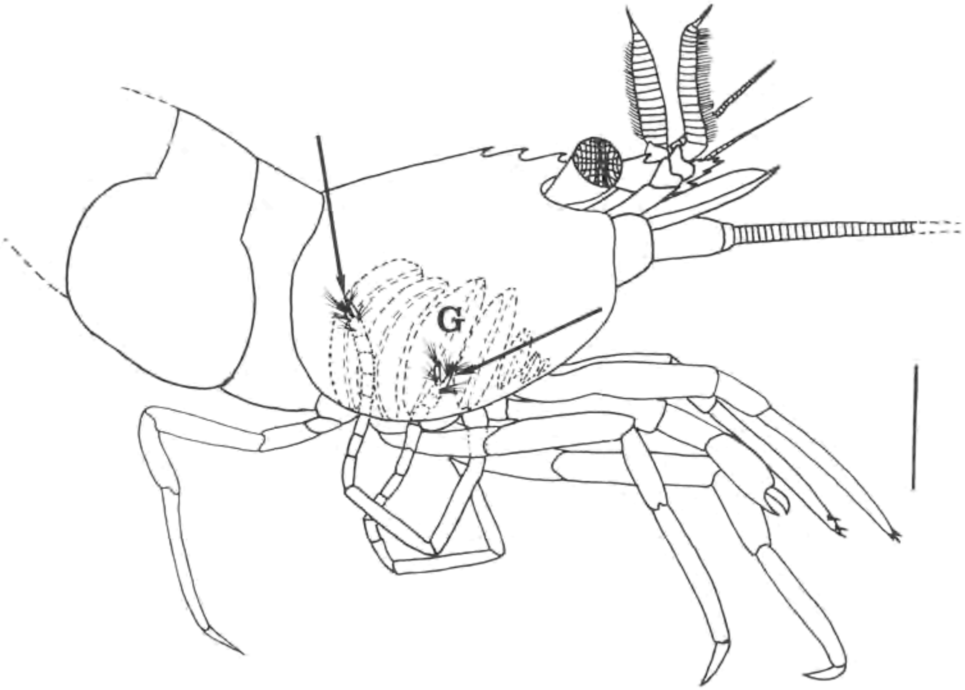

Fig. 3. Gill cleaning by cheliped brushing in the caridean shrimp *Heptacarpus pictus*. Arrows indicated the grooming chelae which are inside the left branchial chamber brushing the gills (G); scale, 2.0 mm.

the Decapoda. [Vuillemin (1967) reviewed some decapod gill cleaning mechanisms, and Bauer (1979) studied gill cleaning in caridean shrimp.] Although decapods periodically flush the gill chamber by reversing the respiratory current, most species possess gill cleaning structures with which the gills are scraped by bristlelike compound setae. Some decapods actively brush the gills with tufts of setae on the grooming chelipeds. In other species, the gills are passively cleaned when compound setae, arising from thoracic limb base processes (epipods or setobranchs), are agitated among the branchiae during feeding, walking, or other leg movements.

Many decapod species clean the gills by cheliped brushing (Table 1; Bauer, 1979 for carideans). Grooming chelae, bearing thick grooming brushes composed of multiscaled or serrate setae, are thrust by the decapod into the gill chamber where the chelae brush and pick through the gill lamellae or filaments (Fig. 3). Several species of caridean shrimps surveyed brush the gills with one or the other pair of chelipeds. All the stenopodid shrimps surveyed used the setose first and second pairs of chelipeds to clean the gills. Except for the axiid thalassinids, the anomurans examined have the last thoracic leg modified as a grooming cheliped (Fig. 4). In the galatheid *Pleuroncodes planipes* and the porcellanid *Petrolisthes*

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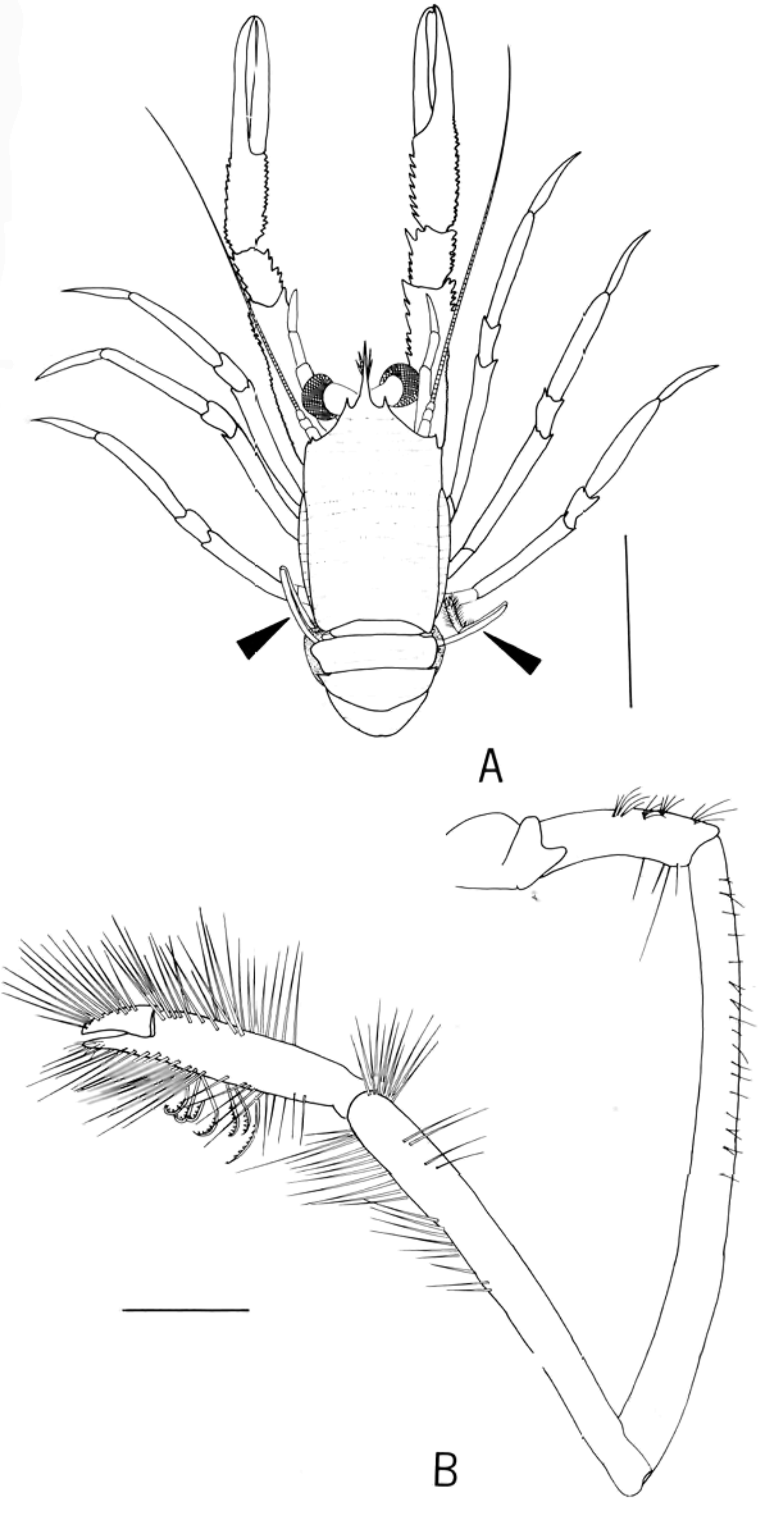
Fig. 4. Grooming chelipeds (pereopods 5) in the galatheid crab *Pleuroncodes planipes:* A, position of grooming chelipeds indicated by arrows (scale, 1.0 cm); B, grooming cheliped of right side (lateral view) (scale, 1.0 mm).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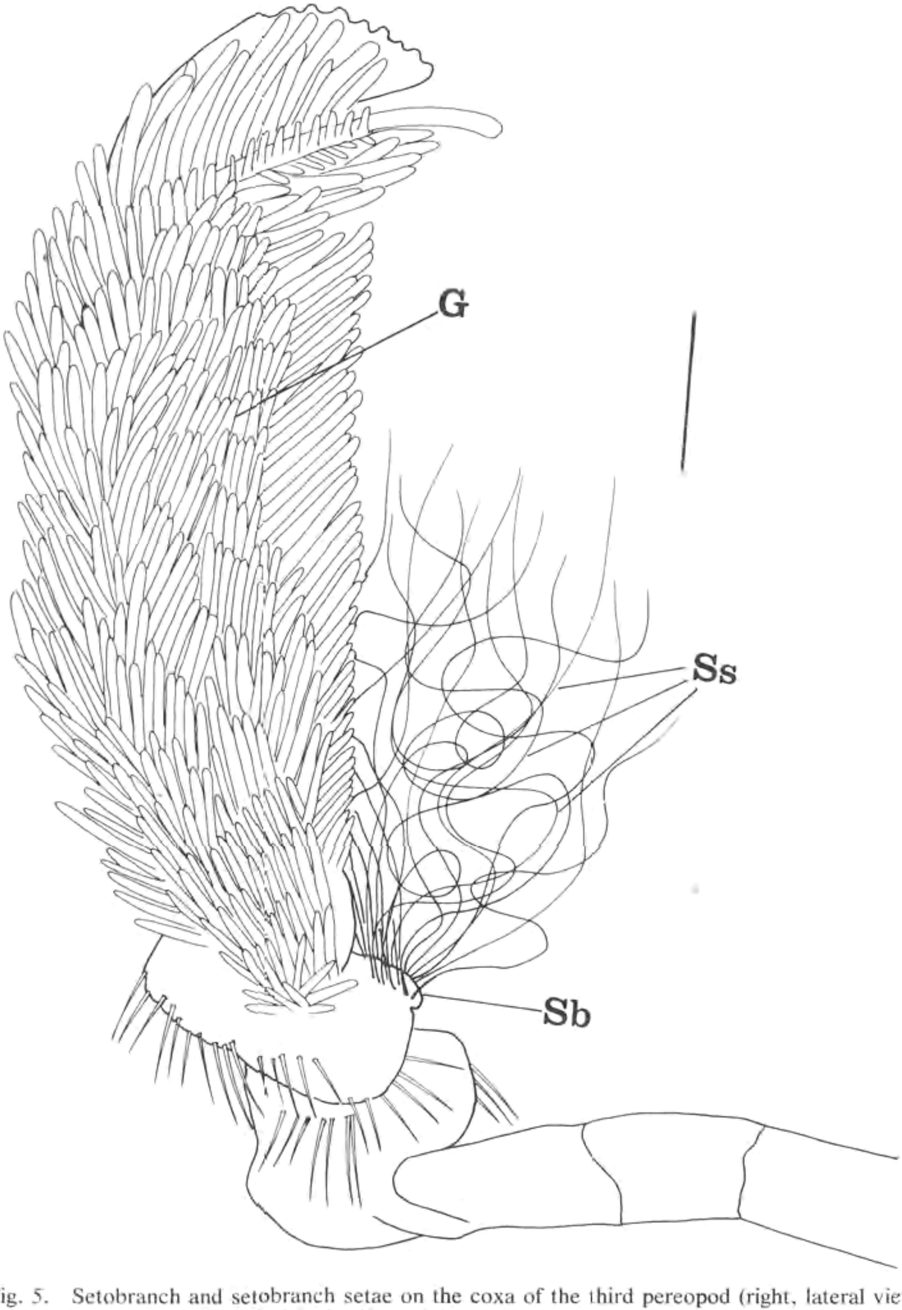

Fig. 5. Setobranch and setobranch setae on the coxa of the third pereopod (right, lateral view) of the crayfish *Procambarus clarkii*. G, gill (podobranch); Sb, setobranch; Ss, setobranch setae; scale, 1.0 mm.

cabrilloi, the carapace is tilted forward so the cleaning chelipeds can reach among and preen the gills.

Other decapods use setobranch setae to perform gill cleaning. Setobranchs are setiferous papillae that are located on coxae of the third maxillipeds and pereopods in many decapod species (Fig. 5; see also Bauer, 1979). Long compound setae reach up among the gills from the setobranchs. When a leg with a setobranch is moved, the setobranch setae are jostled and scraped among the gills, presumably cleaning them. In carideans studied, the ultrastructure of setobranch setae is very similar to that of setae composing the grooming chelae brushes that are used for cleaning the gills (Bauer, 1979). Setobranchs are present in many caridean species, in the astacid crayfishes examined, and in the two axiid anomuran species observed. Caridean epipod-setobranch complexes are unique: the setobranch setae of one leg are guided to the gills by the hooked epipod of the leg anterior to it (Bauer, 1979). Setobranchs are not functionally coupled to the epipods of other decapods surveyed here (Table 1).

Setobranch gill cleaning is apparently a more primitive method of gill cleaning than cheliped brushing. Within the Caridea, the two gill cleaning methods are, in general, mutually exclusive. Although most hippolytids have both mechanisms, the setobranchs show many stages of reduction and loss. Within the hippolytid genus *Heptacarpus*, for example, one finds the entire range of variation from four pairs of epipod-setobranch complexes per species to complete loss of these structures in some species. Cheliped brushing is in the process of replacing hippolytid setobranchs as the gill cleaning mechanism, a process which apparently has also taken place in such families as the Palaemonidae.

Setobranchs of anomurans also appear to have been replaced by cheliped grooming. In the primitive (macruran-like) axiid thalassinids, setobranchs are present. The carapace is firmly fixed around the cephalothorax, and thus the last leg, which is an achelate walking leg, cannot enter the branchial chamber posteriorly for gill brushing as in other anomurans examined. By contrast, the last leg of *Callianassa californiensis* is reduced in size, dorsally bent, and weakly chelate; in addition, the carapace can be lifted so that the last leg can and does brush the gills. These tendencies have progressed further in hippideans, galatheideans, and paguridcans, so that the last leg functions exclusively as a grooming cheliped which is often held within the branchial chamber. All these anomurans brush the gills and lack gill cleaning setobranchs. In the penaeid, palinurid, nephropid lobster, and brachyuran species examined, gill cleaning setae, similar to setobranch setae in structure and placement among the gills, are located on thoracic epipods. Epipods of *Penaeus brevirostris* and *P. merguiensis* on the third maxillipeds and first three pereopods bear compound setae on both sides of the epipodal blades (Fig. 6) which are located among the gills. As with setobranchs, normal movements of the thoracic legs cause the setiferous epipods to be brushed among the gills. However, another penaeid, *Gennadas incertus*, has epipods which are highly reduced and lack cleaning setae. (Perhaps observations on living *Gennadas* spp. will reveal that gill brushing by the setose chelipeds has replaced epipodal cleaning of the gills.) Brachyuran gills are cleaned by setiferous maxillipedal epipods (Table 1; Warner, 1977) (Fig. 7). The epipod of maxilliped 1 lies above (lateral) to the gills, while the remaining maxillipedal epipods are situated beneath (medial) to the branchiae. Whenever the maxillipeds are moved, the setiferous epipods sweep over the gills.

General Body Grooming

Prolonged bouts of general body cleaning are a common feature of many decapod species. General body grooming includes the following cleaning activities: (1) pereopodal brushing of the carapace, thoracic sternites, abdominal pleurites and sternites, and body appendages; (2) cheliped picking and nipping at the body, especially at articular areas between appendages and body segments. In other words, all those preening activities exclusive of antennular grooming by the third maxillipeds, antennal flagellum cleaning by pereopod 1, embryo preening (Bauer, 1979), and gill cleaning are classified under the term general body grooming (cleaning, preening). Cleaning chelipeds usually groom the cephalothorax while posterior pereopods with propodal setal brushes preen the abdomen; however, there can be considerable overlap in areas groomed. Additionally, only chelipeds or only posterior pereopods may groom the body in a particular species (in which general body cleaning takes place).

In the natantian species observed, setose chelae are important general body cleaning limbs. The penaeids preen with all three pairs of chelipeds while stenopodids use only the first two pairs. Except for atyids, which use both pairs of chelipeds, caridean species observed primarily groom with either the first or the second pair of chelipeds (Bauer, 1978). The second and third pairs of chelipeds are used for nipping at the body in the nephropidean lobsters and crayfish; however, these chelipeds are not so extensively used as in natantians. The grooming cheliped of galatheidean, paguridean, and callianassid anomurans has developed from the posterior walking leg of macrurous forms, and this cheliped is used in general body cleaning.

In many caridean (Bauer, 1978), astacuran, and axiid anomuran species, there is a grooming brush on either propodus or dactylus or both of the last or penultimate walking legs (Fig. 8) (Table 1). None of the brachyurans examined had a similar setal grooming brush on the walking legs. The lobster *Panulirus interruptus* grooms the body with the setose dactyls of all the pereopods.

DISCUSSION

Adaptations for preening the chemosensory appendages are invariably present in decapod crustaceans. In most cases, the antennules, which bear the olfactory esthetascs, are groomed by serrate setae on the third maxillipeds. The wide distribution and low morphological-behavioral variation in antennular grooming must be the result of an intense selection pressure that has varied little throughout the evolutionary history of the Decapoda. The antennules are important chemoreceptor sites mediating the detection of dissolved food stimuli and pheromones (Reeder and Ache, 1980; Dunham, 1978). Experimental studies have shown that antennular fouling and subsequent damage to olfactory hairs can occur when grooming is prevented (Bauer, 1975; 1978). It is likely that the relatively uniform mode of antennular grooming has evolved to maintain clean antennular esthetascs that can function properly in the location of food and a potential mate by decapods.

The antennular flagella of decapods are chemotactile in function (Barber, 1961) and appear to be important appendages for gathering environmental information. All the decapods observed alive in this study groom these sensory structures; however, there is a basic dichotomy in antennal cleaning between natant and reptant groups. In a majority of the Natantia (Penaeidea, Stenopodidea, Caridea), there is a very specialized pair of brushes for preening the antennal flagella. Reptants lack these and use only the third maxillipeds.

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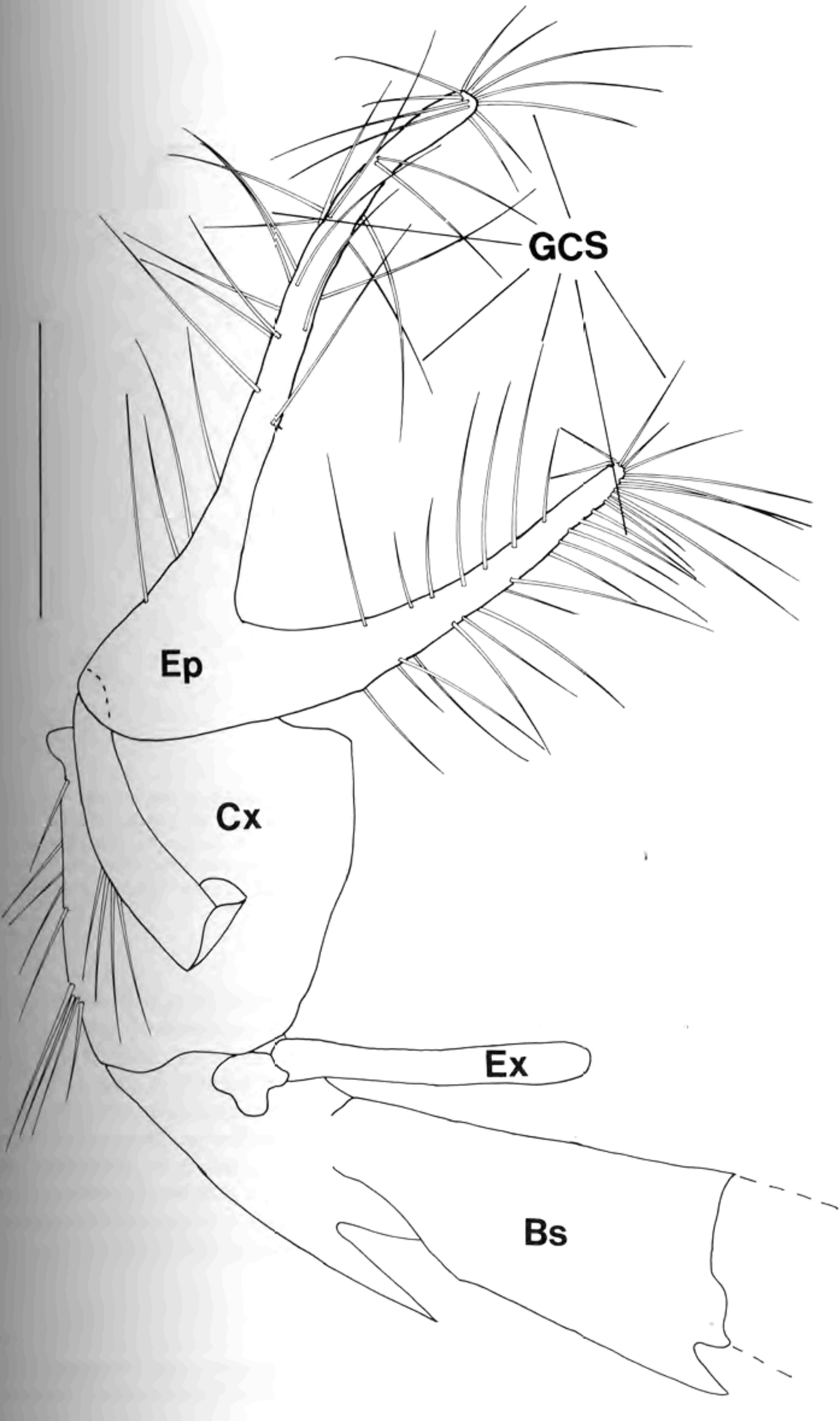
Fig. 6. Gill cleaning epipod of *Penaeus brevirostris* (from the first cheliped, right side, lateral view). Bs, basis; Cx, coxa; Ep, epipod; Ex, exopod; GCS, gill cleaning setae; scale, 2.0 mm; additional setae on basis and ischium not figured for clarity.


GCS
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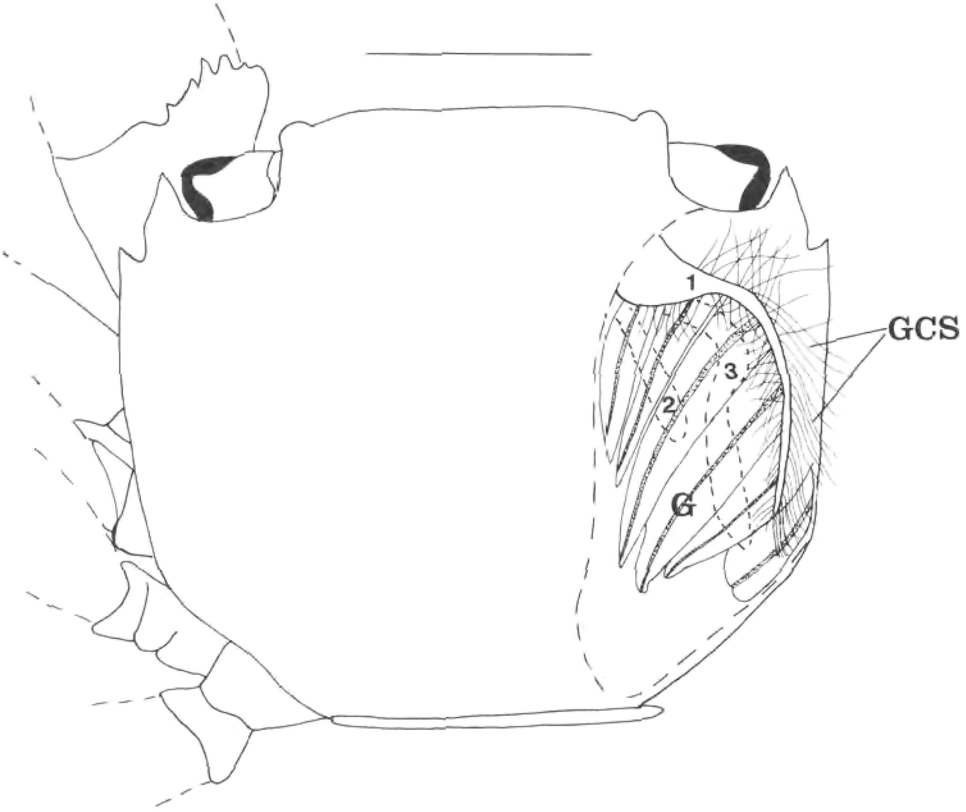

Fig. 7. Maxillipedal gill cleaning epipods in the brachyuran crab *Pachygrapsus crassipes*. A dorsal view of the crab is figured, and the roof of the branchial chamber has been cut away (heavy dotted lines) to show the gills and epipods. The epipod of maxilliped 3 lies above the gills, while the epipods of maxillipeds 2 and 3 lie below. Gill cleaning setae are figured for epipod 1 only. Pereopod bases are figured on the left side only. 1, 2, 3 epipods of maxillipeds 1, 2, and 3 respectively; G, gill; GCS, gill cleaning setae; scale, 1.0 cm.

Perhaps the explanation for this natant-reptant divergence in antennal cleaning is strictly functional. One hypothesis is that the first chelipeds of most reptants are too large and clumsy for this grooming behavior. However, the first chelipeds of penaeideans, stenopodideans, and carideans vary greatly in size, structure, and function. Yet most species in these shrimp groups possess the antennal cleaning brushes; these brushes are always in the same location on the cheliped, show the same function, and have very similar structure. I feel these similarities are too great to be ascribed to parallel evolution. Perhaps a better hypothesis than the functional one is that the antennal cleaning brushes of stenopodidean, penaeidean, and caridean shrimps constitute a derived character that indicates common

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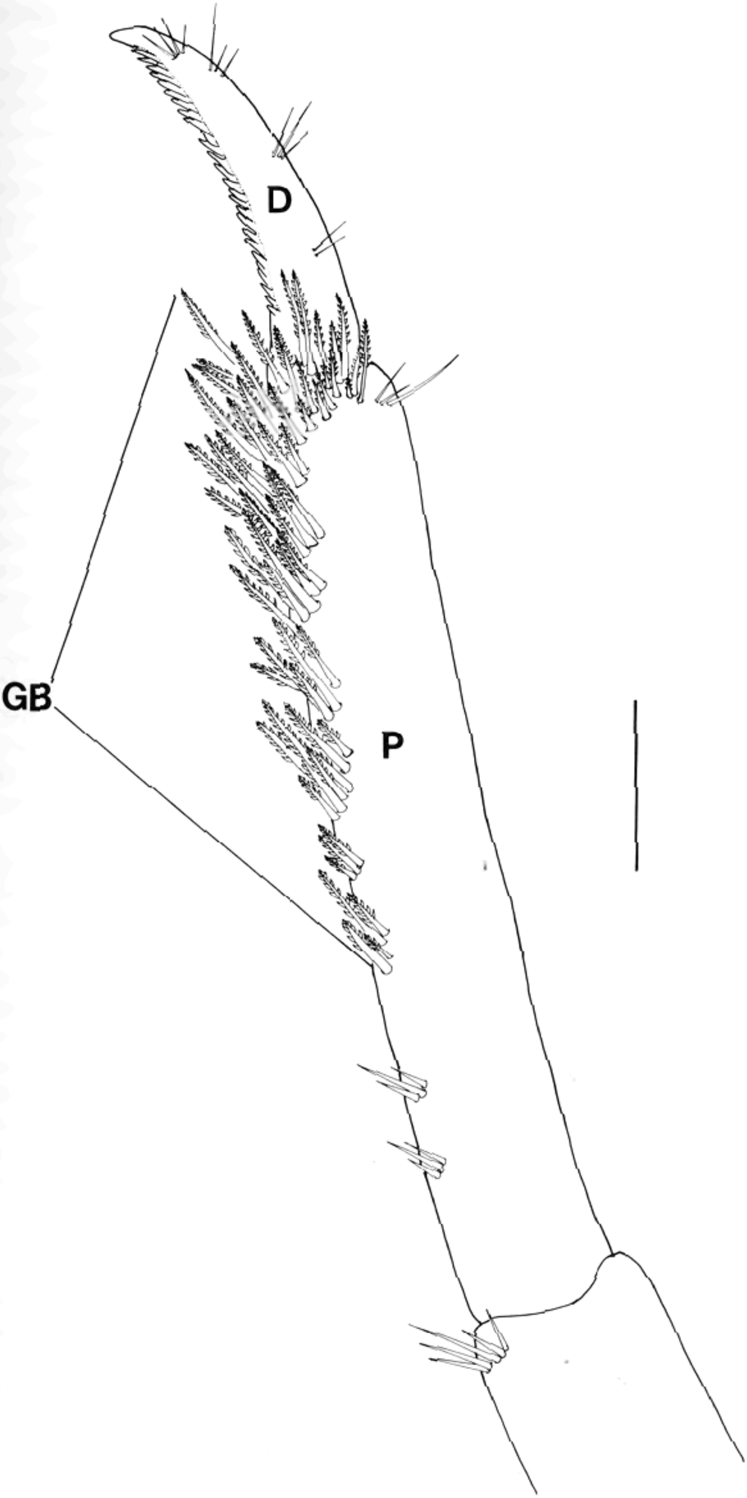
Fig. 8. General body grooming setal brush on the propodus of pereopod 4 (right, ventromesial view) of the crayfish *Procambarus clarkii*. D, dactyl; GB, grooming brush of serrate setae; P, propodus; scale, 1.0 mm.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ancestry for these groups. This character supports the inclusion of all three shrimp groups in the decapod suborder Natantia.

Aside from the flushing of the gill chamber by reversal of the respiratory current, gill cleaning essentially consists of only a single mechanism in the decapod species examined—groups of denticulate or serrate setae that rub over and rasp the gills. However, the means by which these compound setae are placed into contact with gills is variable. The setae may be on cheliped tips, setobranchs, or thoracic epipods. The ubiquity of gill cleaning devices in decapods is an obvious result of selection pressure to maintain clean gill surfaces (within the confines of a branchial chamber) for efficient exchange of respiratory gases.

Although grooming of sensory appendages and respiratory surfaces is widespread throughout the decapods, preening of the other body surfaces (general body grooming) is frequently not well-developed. In the natantian shrimps, body preening is a common or prolonged behavior; chelipeds and other pereopods are often specialized for grooming. At the other extreme, the brachyuran crabs observed spend little or no time in body preening, and pereopodal specializations for grooming are lacking. Schöne (1961) also has noted this difference in "body care" between shrimps such as *Palaemon* and *Palemonetes* and the brachyuran crab *Carcinus*. As might be expected, epizoic fouling occurs more frequently on brachyuran species than on natantian. In my experience, shrimps are rarely fouled, whereas some brachyuran species suffer varying degrees of fouling, sometimes quite heavy, by sessile invertebrates and algae (see also Wolff, 1958). In some majid crabs, fouling is actively promoted as a camouflage (Getty and Hazlett, 1978; Wicksten, 1980). Macruran and anomuran species show great variation in general body grooming and the extent of fouling between the natantian and brachyuran extremes. Anomuran species such as the red crab *Pleuroncodes planipes* and the porcelain crab *Petrolisthes cabrilloi* clean vigorously and exhibit little fouling (unpublished observations); macruran lobsters can be severely plagued by epizoic fouling (Kaestner, 1974).

The reduction of general body grooming within the Decapoda may have accompanied the group's major evolutionary trend, i.e., the change from the shrimplike (caridoid) form to the crablike (brachyurous) facies. The caridoid facies of natantians is a set of adaptations for swimming; by contrast, both the forward and backward (escape) swimming of shrimps have been replaced by efficient walking and running in the Brachyura. A whole series of morphological modifications have made possible this important transformation in locomotion and life style: dorsoventral flattening and lateral expansion of the cephalothorax; reduction in the size and musculature of the abdomen, and the folding of the abdomen beneath the cephalothorax; alteration in pleopod function from swimming to reproduction; loss of the uropods and retrograde escape swimming by rapid abdominal flexion; and loss of the long keeled rostrum and rudderlike antennal scales (Calman, 1909; Glaessner, 1960). Macruran and anomuran decapods show several intermediate morphological and locomotory states between the natantian and brachyuran end points.

I have suggested that epizoic fouling could increase drag and decrease swimming capability (Bauer, 1975; 1978). Natant decapods are characterized by adaptations for body streamlining. I believe that general body grooming is well-developed in shrimps because such cleaning prevents fouling that would interrupt streamlining and interfere with swimming. Conversely, general body grooming behavior and morphology is poorly developed in the Brachyura, an assemblage of ambulatory species. The typical brachyuran body form is not streamlined, and thus there has been lower selection pressure to maintain general body grooming. It is interesting to note that in the one portunid crab species for which I have observations, body cleaning is a frequent activity. Portunids are brachyurans that have, in many species, secondarily reacquired swimming behavior. It seems reasonable that a similar selection pressure, i.e., increased drag due to fouling, is acting on these portunids as on swimming natantians. As a result, portunids, such as *Callinectes sapidus*, engage in intense bouts of body cleaning as do shrimps. However, unlike shrimps, portunid appendages do not appear specialized for general body cleaning.

Although more brachyurans show epizoic fouling than do natantians, many brachyuran (and other decapod) species that lack general body cleaning remain quite clean. This suggests the operation of antifouling mechanisms besides mechanical self-grooming. Certainly, molting completely removes fouling material. But molting cannot occur often enough to serve as the only means of preventing fouling. Molting is an energetically expensive process, and it exposes the molter to death from physiological stress and predation. Periods between molts can be several months long in adult decapods, particularly during periods of poor food supply or low temperature. Females brooding embryos cannot molt until after the embryos hatch. In long intermolt periods, a considerable community of fouling organisms can build up in the absence of grooming or some other antifouling mechanism.

One alternative to grooming behavior might be the burrowing behavior of many decapod species. For example, the shamefaced crabs (*Calappa* spp.) bury themselves in sand or mud (Kaestner, 1974). Raninid, albunid, and hippid crabs are burrowing decapods. Abrasion of the exoskeleton and smothering by sediment would greatly deter epizoic fouling.

Many decapod species wedge themselves under stones and in narrow crevices; fouling organisms growing on the exoskeleton could be scraped off or injured by rough surfaces. Smaldon (1974) attributed a lower amount of fouling on the dorsal surface of a porcellanid crab to this factor.

Glynn (1970) showed that sphaeromatid isopods (which lack general body grooming) became disastrously fouled by algae when they were prevented from hiding away from sunlight. He suggested that their normal nocturnal activity pattern might be an adaptation to avoid fouling by algae. In like manner, some decapod species might deter (perhaps incidentally) algal fouling by cryptozoic or nocturnal habits.

Terrestrial or amphibious crabs are obviously under reduced epizoic fouling pressure. Opportunities for settlement of epizoites are low or absent, and any fouling organisms managing to settle on these crabs would have serious dessication and feeding problems. Crane (1975) reported that fiddler crabs (*Uca* spp.) that were muddy from digging rid themselves of sediment by plunging into the standing water of their burrows.

Fouling pressures vary in different habitats. Wolff (1958) reported reduced fouling on oxyrhynchous crabs that inhabited a rocky reef kept clean by strong currents. Apparently, the high current strength prevented successful larval settlement of sessile organisms in this location. In another example, Norse and Estevez (1977) reported that epibiontic fouling of euryhaline portunid crabs (*Callinectes* spp.) was greater in marine than in estuarine or freshwater habitats. However, stenohaline marine portunids showed little fouling. The explanation for these differences was not known.

There is a need for increased study of cleaning behavior in decapods. Grooming structures are described from only a very small proportion of the several thousand decapod species. Experimental studies similar to those of Bauer (1979) are necessary to confirm the presumed cleaning function of structures such as setobranchs and setiferous pereopodal epipods. Little observational and experimental evidence on alternative methods to mechanical self-grooming is available. Such mechanisms could be rewarding subjects of research. (For example, one possibility not yet investigated is that antifouling chemicals are secreted on the surface of the exoskeleton by the tegumental glands.) A comprehensive knowledge of grooming in decapods could be important in understanding the ecology and behavior of decapod species. For example, Hubbard and Pocock (1972) showed that coral species which were best adapted, morphologically and behaviorally, in rejecting sediment occurred in areas of high sedimentation, whereas species less able to clean themselves were distributed in less turbid areas. These workers then used morphology of fossil species to infer environmental (sedimentary) properties of ancient habitats. The study of Glynn (1970) on isopods indicated that crustacean activity patterns could be related to the fouling pressures of the habitat.

Grooming structures should be very useful in phylogenetic studies. The relationship of the Penaeidea, Caridea, and Stenopodidea, for example, is still not clear (Glaessner, 1969). The widespread distribution of antennal cleaning brushes on pereopod 1 in these groups is one character that must be considered in deciding this issue. The question of monophyly vs. polyphyly in the Brachyura is far from settled (Rice, 1980); study of the gill cleaning mechanism of brachyurans might clear up some of the confusion. The characteristic cleaning cheliped of anomurans such as callianassids, pagurideans, hippideans, and galatheideans is a character that supports, in my view, the close relationship of these groups. At lower taxonomic levels, too, variations in grooming characters may be quite useful in establishing phylogenies. One advantage of using grooming characters is that their function is either known or can be determined experimentally. This knowledge is important when one tries to decide whether joint possession of a character by two groups is because of common ancestry or parallel evolution.

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