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STOMATOPOD GROOMING BEHAVIOR: FUNCTIONAL MORPHOLOGY AND AMPUTATION EXPERIMENTS IN *GONODACTYLUS OERSTEDII*

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ABSTRACT

Qualitative and quantitative observations on *G. oerstedii* show that its grooming behavior consists (in order of decreasing frequency) of antennae (A1 and A2), eye, subcarapace, gill, and general body grooming. As in decapod crustaceans, there is an inverse relationship between bout frequency and bout duration of grooming behaviors in this stomatopod. The only appendage observed in grooming, the first maxilliped, has grooming brushes of rasp, multiscaled, and scaled serrate setae; the microstructure of these setae is described and illustrated with SEM. In the Stomatopoda, low diversity of specialized grooming structures reflects a conservative stomatopod body plan, while the high diversity of cleaning characters in the Decapoda reflects the group's high variation in body morphology. Analysis of the functional morphology of *G. oerstedii*'s fifth maxilliped (M5) propodal brush suggests that it is a reduced and vestigial grooming character. It is concluded that a vestigial M5 grooming brush is a synapomorphy that supports the hypothesis by Jacques (1983) that the Gonodactylidae, Odontodactylidae, and Protosquillidae are closely related.

Amputation experiments were performed to test the hypothesis that grooming behavior is an antifouling adaptation. Members of the experimental group had the first maxillipeds amputated; in control groups, exopods of the third pereiopods, a nongrooming appendage, were ablated. Experimental and control animals were exposed to fouling on sea-water tables for 2 weeks. Fouling was quantified by counting strands of *Leucothrix*, a filamentous bacterium. Both gill filaments and antennular aesthestascs of experimental (nongrooming) stomatopods were heavily fouled by *Leucothrix* and other bacterial growth after 2 weeks, while those of controls remained clean. The low fouling on eyes and lack of fouling on most other body surfaces in experimentals raises the possibility that some parts of the exoskeleton may be protected from microbial fouling by the secretion of antifouling compounds.

The importance of grooming behavior in the life of crustaceans has become apparent in recent years. Many crustacean species have compound setae, organized into brushes and combs, that are specialized for scraping and brushing the exoskeleton. Amputation experiments have demonstrated that a major function of grooming is prevention of epibiotic fouling of sensory receptors, gills, embryos, and general body surfaces (Bauer, 1975, 1977, 1978, 1979; Felgenhauer and Schram, 1978; Pohle, in press). Publications dealing with grooming behavior and morphology have concentrated on the decapod crustaceans (Bauer, 1975, 1977, 1978, 1979, 1981, in press a; Felgenhauer and Schram, 1978, 1979; Felgenhauer and Abele, 1983; Holmquist, in press; Martin and Felgenhauer, 1986; Pohle, in press). However, Holmquist (1982, 1985, in press) has also dealt with grooming behavior and morphology in amphipods and isopods.

Stomatopod crustaceans frequently can be observed grooming the body, and the first maxillipeds (first thoracopods) are considered by stomatopod workers to be primarily grooming appendages (Kunze, 1981). In spite of the possible importance of cleaning behavior in stomatopod biology, the literature on stomatopod grooming is virtually nonexistent. Giesbrecht (1910) described and figured grooming positions in *Squilla mantis,* while various workers have briefly remarked on the frequency or possible significance of grooming (Kunze, 1981; Montgomery and Caldwell, 1984; Reaka, 1975, 1978, 1979; Reaka and Manning, 1981). Jacques (1981, 1983) has made valuable contributions on the microstructure of setae in

presumed grooming brushes. Most recently, Morin *et al.* (1985) and Burgni and Ferrero (1985) have dealt with stomatopod grooming from a neurophysiological point of view.

In this report, I give the results of studies on grooming behavior and its adaptive value in the tropical stomatopod *Gonodactylus oerstedii* Hansen, 1895. I describe grooming behaviors and their organization in *G. oerstedii*, document and illustrate microstructure of grooming setae, and give results of amputation experiments on grooming appendages. Part of this work is summarized in a brief report published in conjunction with the First International Symposium on Stomatopod Biology in Trieste, Italy, 1985 (Bauer, in press b). The present report contains more extensive observations on grooming behavior, quantitative observations on behavioral organization, description and illustration of setal microstructure with scanning electron microscopy (SEM), and quantitative analysis and SEM illustration of amputation experiments.

Materials and Methods

Collection of *G. oerstedii* took place in sea-grass (*Thalassia testudinum*) meadows in Puerto Rico and Belize. Most individuals were obtained by breaking open the lower parts of fire coral (*Millepora* sp.) colonies occurring on meadows. *Gonodactylus oerstedii* often make their chambers within the mass of sediment, algae, sponges, tunicates, and other sessile invertebrates in which the base of the coral colony is embedded. *Gonodactylus oerstedii* used for experiments and qualitative behavioral observations were taken in April, June, and July 1985, from shallow sea-grass meadows within 1 km west and south of Cayo Caballo Blanco, near the University of Puerto Rico, Mayagüez, Isla Magueyes Marine Laboratory, at La Parguera, Puerto Rico. *Pseudosquilla ciliata* (Fabricius, 1787), collected for comparative morphological study, were taken incidentally and occasionally with *G. oerstedii* and also by pushnet in sea-grass meadows. Quantitative behavioral observations were done on *G. oerstedii* taken from meadows on the west side of Little Dipper Cay of the Twin Cays complex, 2 km northwest of Carrie Bow Cay, 22 km southeast of Dangriga, Belize (Rützler and Macintyre, 1982).

Observation and photography of cleaning behavior of *G. oerstedii* took place on stomatopods in aquaria on sea-water tables at the Isla Magueyes laboratory. Stomatopods were placed individually in small aquaria with coral sand and a large piece of coral rubble. The animal usually made a partial burrow or situated itself between the piece of coral rubble and the aquarium wall. These stomatopods appeared inactive at night; behavioral observations were taken during the day. Photographs for illustration of cleaning movements were taken with a 35-mm camera equipped with a 50-mm lens, extension tubes, and a strobe light with 1/1500-s flash duration; color transparency film was used. Illustrations of grooming movements were made by projecting transparencies and tracing directly from them.

Quantitative behavioral observations were taken on *G. oerstedii* at the Smithsonian Institution's facility at Carrie Bow Cay in May 1986. Stomatopods were maintained individually in small aquaria with coralline algae (*Halimeda opuntia*) at least 24 h prior to recorded observations. The frequency and duration of grooming behaviors were recorded for 1 h for each individual ($N = 20$ individuals) in daytime observations. Single acts such as antennular preening, eye scrubbing, and rapid acts of other grooming behaviors that occupied some unmeasured fraction of a second were recorded as acts of 1-s duration. Bouts with a duration of greater than 1 s were measured with a stopwatch to the nearest second.

Examination of appendage and setal morphology was done with light microscopy and SEM. Specimens used for SEM were initially preserved in 10% sea-water Formalin, dehydrated through a standard alcohol series to 100% ethanol, critical-point dried, and sputter-coated with a 100 Å thickness of gold or gold-palladium. Specimens selected for morphological examination with SEM were cleaned by sonication, but material from amputation experiments was not sonicated prior to SEM examination. SEM observations were principally carried out at the University of Southwestern Louisiana's Electron Microscopy Center; preliminary SEM work took place at the University of Puerto Rico, Rio Piedras, SEM facility.

Amputation experiments were carried out on *G. oerstedii* at the Isla Magueyes laboratory during June and July 1985. The hypothesis tested was: Does epibiotic or sediment fouling occur on body parts that are not groomed as a result of first maxilliped amputation? The carpus, propodus, and dactylus of the first maxillipeds (thoracopods 1), the observed grooming appendages, were removed from individuals of the "experimental" group, while in the "control" group, the exopods were ablated from the third pereiopods (thoracopods 8). The intention of the latter amputation was to subject

control and experimental individuals to the same experimental trauma. Amputations were done with fine forceps on stomatopods restrained under a dissecting microscope. After operations, most (30 of 33) individuals soon recovered completely on return to sea water. During the experiments, stomatopods were exposed to ambient fouling in a flow-through sea-water system. Individuals were maintained separately in plastic tubs (8-cm diameter, 8-cm height) perforated with 3-mm holes for water circulation. A 6-cm long, 1.3-cm diameter piece of opaque or transparent tubing was placed in each container; the stomatopods used the tubing as shelters.

Two amputation experiments were conducted. Since the light intensity that the day-active *G. oerstedii* normally encounters was not known, I decided to use two extremes in light level, an important factor in algal fouling. The first experiment ran from 7–22 June 1985, and is termed the "Dark" experiment (N = 10 experimentals, 8 controls) because the stomatopod containers were covered by a sheet of black fiberglass screen (2-mm mesh) which greatly reduced light levels in the containers; additionally, pieces of plastic tubing provided as shelters were opaque to light. In the "Light" experiment (13–27 July 1985; N = 5 experimentals, 7 controls), stomatopod containers were covered by a clear plastic sheet perforated with 3-mm holes to admit air; transparent tubing was provided for shelters. The outdoor water tables on which the experiments took place were beneath a roof, so that direct sunlight shone into the containers only for 15–20 min in the early morning. Stomatopods were fed chopped pieces of shrimp every other day. When experiments were terminated, the stomatopods were preserved in 10–15% buffered sea-water Formalin.

Fouling was measured on one antennular flagellum, eye, pleopodal gill filament, and uropodal setae of stomatopods used in experiments. In the first three body parts, strands of the microbial fouling organism *Leucothrix* (Johnson *et al.*, 1971; Sieburth, 1975; Johnson, 1983) were counted. The antennular flagellum bearing the aesthetascs was removed, mounted in water, and viewed at 100× with a light microscope. The number of strands of *Leucothrix* that could be distinguished were counted. Because the bacterial threads were twisted about each other, repeated counts on the same specimen were often slightly different. Therefore, 3 counts were taken on each specimen, and the median of the three is reported here. A similar procedure was used in counting *Leucothrix* on the eye and gill. To measure gill fouling, the gills were removed from the right third pleopod; one group of attached filaments was mounted on a slide and viewed at 100×. Fouling on the middle filament was measured. Uropodal setae displayed complicated sediment and microbial fouling, and *Leucothrix* or other easily counted organisms were difficult to distinguish. For uropodal setae, a qualitative scale was used to characterize fouling (1 = none; 2 = light; 3 = moderate; 4 = heavy). The rank sum test (Wilcoxon T-test; Mann-Whitney U-test) (Tate and Clelland, 1957) was used to test the null hypothesis of no difference in medians between treatments.

Results

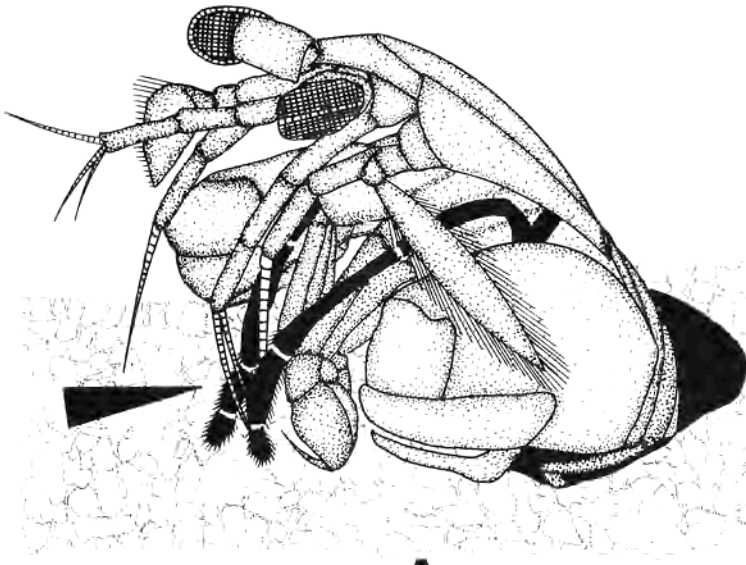
Behavior

Gonodactylus oerstedii preens body parts with the carpus and subchela (propodus and dactylus) of the first maxillipeds. The following grooming behaviors were observed and are described: antennae, eye, subcarapace, gill, general body, and autogrooming.

Antennae Grooming.—This behavior is the preening of the antennules (A1) and second antennae (A2). Antennules may be groomed alone, but when the antennal (A2) flagellum is groomed, it is always together with the antennular flagella. During an act of antennae grooming involving both A1 and A2 (Fig. 1A), the A1 of one side is lowered towards the midline together with the A2 flagellum and peduncle. At the same time, the first maxillipeds (M1) reach up and scrub down the appendages, from peduncle to flagellar tips, from one to several times.

Eye Scrubbing.—The M1 pair reach up and vigorously scrub one or both eyes from one to several times (Fig. 1B).

Subcarapace Grooming.—This refers to apparent M1 grooming of maxillipeds 2–5, maxillipedal epipods, and other areas below the carapace. This category includes observable M1 grooming of another maxilliped (Fig. 2A) and rapid movements of the reflexed M1 pair below the carapace or among the maxillipeds where it is difficult to observe which body part is being cleaned. Frequently, maxillipeds 3–



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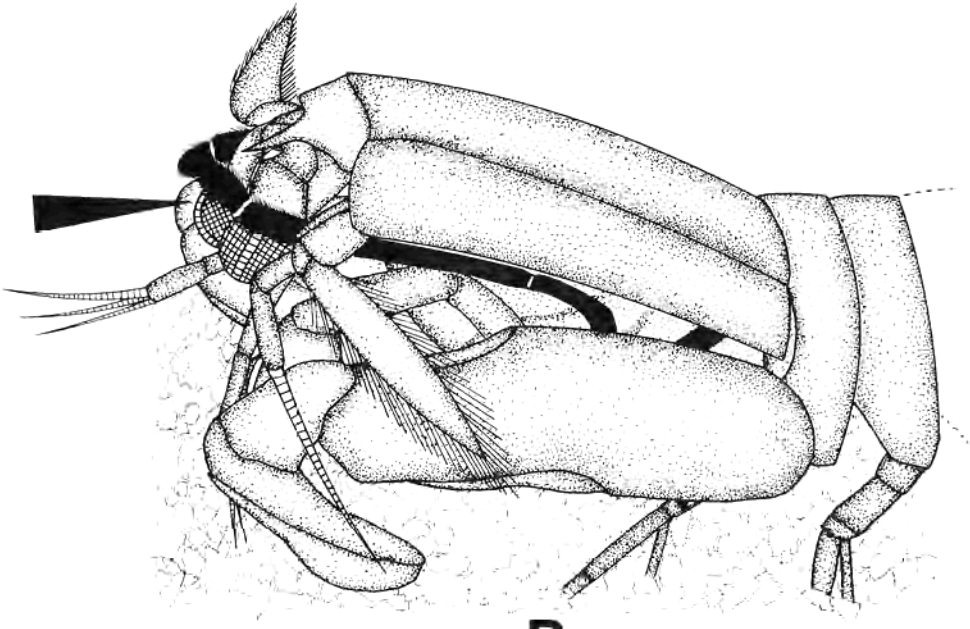

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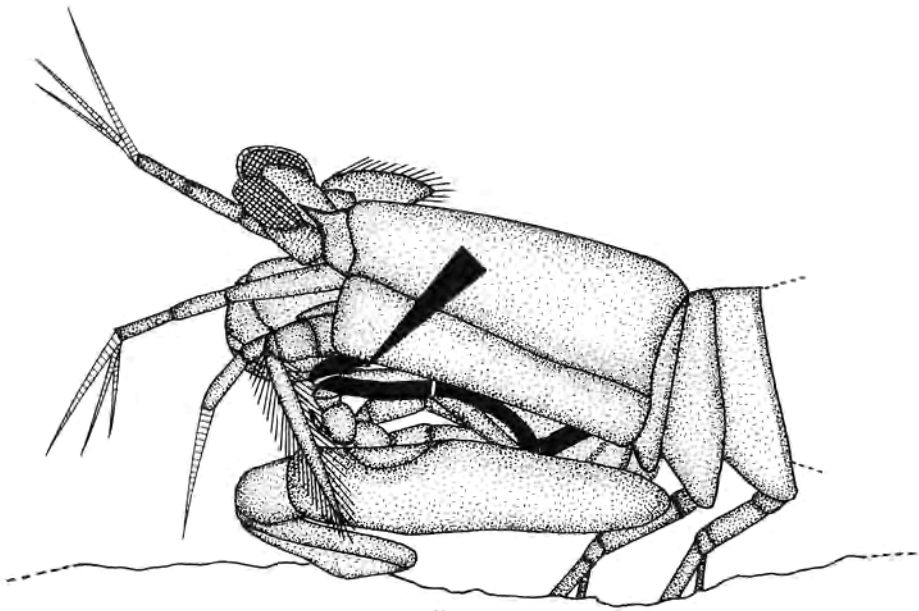
Fig. 1. *Gonodactylus oerstedii*. A. Partially emerged from burrow in sand-gravel substratum, grooming (arrowhead) the antennular and antennal flagella with first maxillipeds (in black). B. Scrubbing (arrowhead) of both eyes with first maxillipeds (in black).



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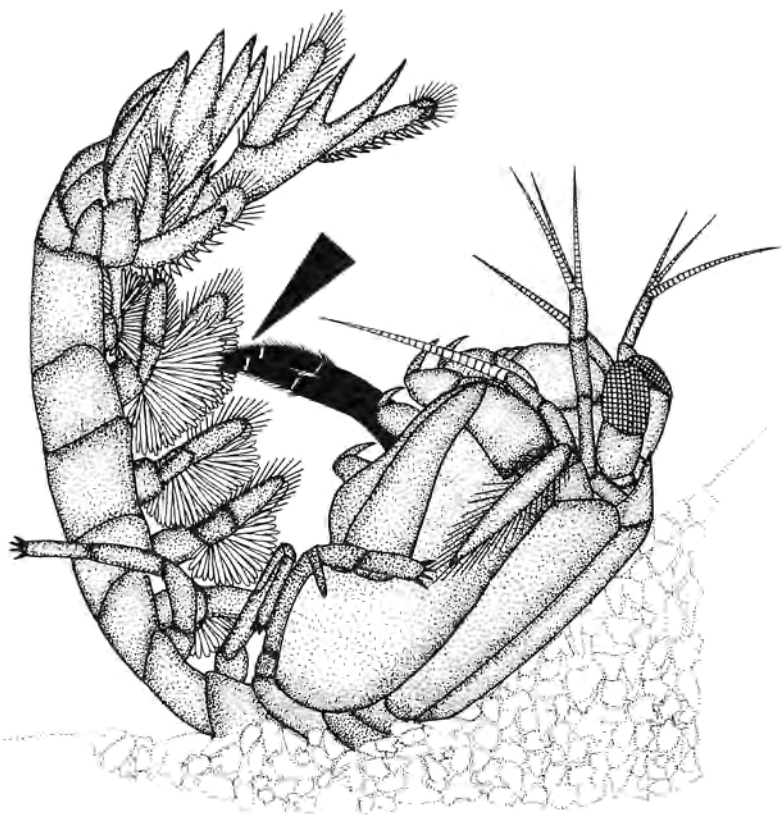

B

5 move rapidly together when one of these pairs is apparently being groomed by the first maxillipeds.

Gill Grooming.—The stomatopod reaches back among the pleopodal gills and rapidly brushes up and down among their filaments with the M1 pair (Fig. 2B). The stomatopod curls its body, either in a normal upright position or upside down (Fig. 2B), so that the M1 pair can reach the gills.

General Body Grooming.—This is the unspecialized cleaning of a variety of body surfaces (Bauer, 1981). This behavior was rarely noted in *G. oerstedii.* I have observed grooming of the rostral plate, the lateral surface of the raptorial appendage, and the dorsal and lateral surfaces of the anterior abdominal segments. This is the only grooming behavior in which the left and right first maxillipeds do not typically groom a body part in unison. Each member of the M1 pair may scrub and brush different, although closely situated, body parts.

Embryo Grooming.—Females hold an embryo mass with all the maxillipeds, which frequently jostle and knead the embryos. The M1 pair appears to brush and scrub among the embryo mass.

Autogrooming.—This behavior is the brief rapid mutual grooming of the left and right first maxillipeds. It occurs after all the above described grooming behaviors, and thus it may be considered the terminal act in any bout of grooming behavior.

Quantitative observations on the frequency and duration of bouts (=one to several acts) of various grooming behaviors are summarized in Table 1 for a group of 20 *G. oerstedii,* each observed for a 1-h period. Antennae grooming was by far the most frequent grooming behavior, while other grooming of the cephalothorax (eye, subcarapace) ranked second and third in frequency. Gill and especially general grooming were infrequent. Bouts of the higher frequency grooming behaviors (antennae, eye, and subcarapace) usually consisted of one to few acts and were of short duration (approximately 1 s) (Table 1). Gill and general body grooming were infrequent, but, when they occurred, were longer in duration. Only one female from the group of individuals observed was brooding embryos; 27 bouts of embryo cleaning occurred in the 1-h observation period, with a median duration of 2 s (range, 1–31 s). The percentage of time spent in grooming by individual stomatopods was calculated for all grooming behaviors listed in Table 1. The median time spent in grooming was 0.9% of total time observed (range: 0–8.4%), with no grooming observed in two individuals.

Morphology

The propodus and carpus (Fig. 3A, B) of the first maxillipeds, the grooming appendages of *G. oerstedii,* are furnished with a wide array of setae modified for scraping and brushing the exoskeleton. Three major types of compound setae are organized into grooming brushes on the first maxillipeds. Scaled serrate setae are set in numerous rows along the medial side of the carpus (Fig. 3A, C). In each seta, a row of long, finely serrate tooth setules is set opposite an identical setal row on the setal shaft (Fig. 3D, E). The opposite side of the seta is covered with long digitate scale setules (Fig. 3D, E) whose tips point toward the tip of the seta.

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Fig. 2. *Gonodactylus oerstedii.* A. Subcarapace grooming. Here, first maxilliped (in black) is cleaning (arrowhead) merus of third maxilliped. B. Brushing (arrowhead) of gill filaments with first maxillipeds (in black).

Table 1. Bout frequency and bout duration of grooming behaviors from 1-h observation periods of 20 *Gonodactylus oerstedii*. Frequency measurements refer to all 20 individuals. Duration measurements apply only to individuals in which a given behavior took place and for which a bout duration could be measured. The number in parentheses after the range for bout duration is the number of individuals in which the behavior was observed. For each individual in which a particular behavior took place, the average ($\bar{x}$) bout duration of that behavior was calculated, and the median and range of those values are given below.

	Bout frequency (no./h)		Bout duration (s)	
Grooming behavior	Median	Range	Median	Range
Antennae grooming	21.5	0–61	1.0	0 (20)
Eye scrubbing	3.0	0–21	1.0	1.0–1.3 (16)
Subcarapace grooming	2.0	0–42	1.1	1.0–3.5 (11)
Gill grooming	0	0–20	6.8	6.2–8.7 (4)
General body grooming	0	0–9	5.0	1.0–7.0 (3)

The serrate tooth setules appear to be a variation of the scale setules in which the setule is finely toothed rather than digitate and is directed out away from the setal shaft. The tip of the seta bears several, closely set, strong bladelike setules that form an apparent scraping structure (Fig. 3E).

A second setal type ("multiscaled") involved in grooming on the first maxillipeds consists of long setae whose distal halves are clothed with a dense covering of digitate scale setules (Figs. 3A, B, F; 4A, B). These scale setules are proportioned differently than those on the carpal setal rows, and are somewhat shorter and wider than those of the latter. Major brushes of multiscaled setae originate distally on the carpus (Fig. 3A, B) and those on the medial side of the limb extend across the medial surface of the propodus. Smaller groups of multiscaled grooming setae are situated near the propodal-dactylar articulation (Fig. 3A, B), along the inferior (flexor) margin of the carpus, and on the distomedial end of the merus. Similar setae (Fig. 4C), sparsely distributed and with rudimentary development of scale setules, are located more proximally on the first maxillipeds and elsewhere on remaining maxillipeds.

A third major grooming brush is located along the superior (=extensor) margin of the propodus (Figs. 3A, B; 4D). The brush is composed of setae that Jacques (1981, 1983) has termed "soies en râpe," or rasp setae. These setae occur in no other location on *G. oerstedii*. Each stout seta is naked proximally up to an annulus circling the setal shaft. Distally, there is a double row of small pointed tooth setules (Fig. 4E, F) on one side of the shaft, while the remainder of the shaft is densely covered with unique small scale setules (Figs. 4E, F; 5A). The scale setules have 2 or 3 digitations on the side of the seta opposite the double row of tooth setules, but grade into single-bladed setules in the area approaching the tooth setules (Figs. 4F, 5A).

Another setal type possibly concerned with grooming is located on the distal end of the extensor margin of the propodus, near the tip of the reflexed dactyl (Fig. 4D). These large setae, 4–7 in number, are serrate, with a double row of large tooth setules; there is no other setulation (Fig. 5B). Jacques (1981, 1983) has termed them "soies à dents en double peigne" (double comb setae).

An accessory grooming brush on the propodus of the fifth maxillipeds is known in many stomatopods (Giesbrecht, 1910; Jacques, 1981, 1983; Morin *et al.*, 1985). I examined all the maxillipeds, looking for possible grooming brushes, and, as Jacques (1983) has noted for *Gonodactylus* spp., there is a setal group on the propodus of the fifth maxillipeds (M5) with the compound setulation typical of

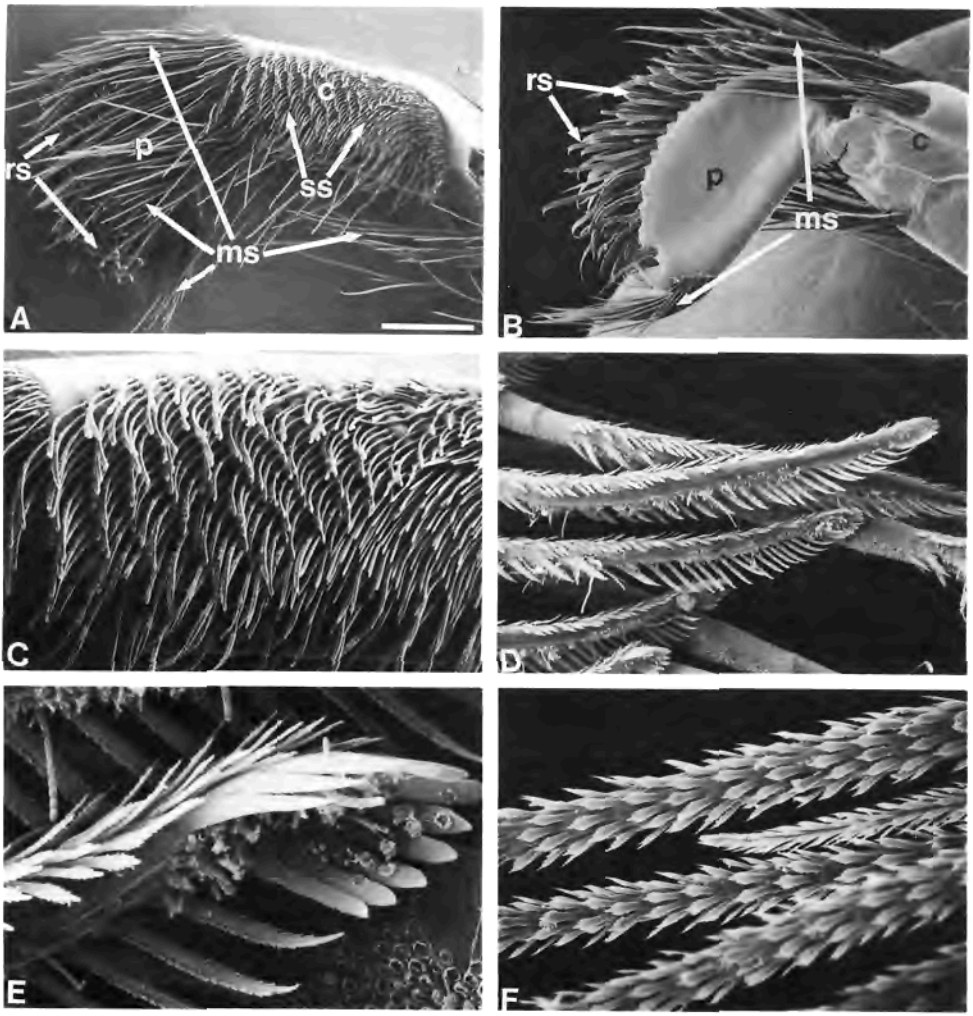

Fig. 3. *Gonodactylus oerstedii*. A. Arrays of grooming setae on medial surface of first maxilliped (M1); c = carpus; p = propodus; ms = multiscaled setae; rs = rasp setae; ss = scaled serrate setae; scale marker = 840 μm. B. Lateral view of M1 terminal segments; c = carpus; p = propodus; ms = multiscaled setae; rs = rasp setae; scale marker in A = 520 μm here. C. Medial view of M1 carpus, showing rows of scaled serrate setae; scale marker in A = 300 μm here. D. Scaled serrate setae from M1 carpus; scale marker in A = 40 μm here. E. Tip of scaled serrate seta from D; scale marker in A = 10 μm here. F. Portions of setal shafts of multiscaled setae from distosuperior carpal brush shown in B; scale marker in A = 23 μm here.

grooming setae (Fig. 5C–F). Although M3–5 subchelae (propodus and dactylus) are similar in morphology and in function (food-handling), a compound setal group occurs only on M5. The absence of a grooming brush on the fourth maxilliped is illustrated in Fig. 6A, B (compare to Fig. 5C, D). Setae in the M5 brush of *G. oerstedii* are beset with digitate scale setules whose structure is reminiscent of multiscaled setae on the first maxilliped (compare Fig. 5E, F with Figs. 3F; 4A, B). The M5 brush of *G. oerstedii* is small, as in other Gonodactylidae, Odontodactylidae, and Protosquillidae (see Jacques, 1983; Kunze, 1981). The M5 brush

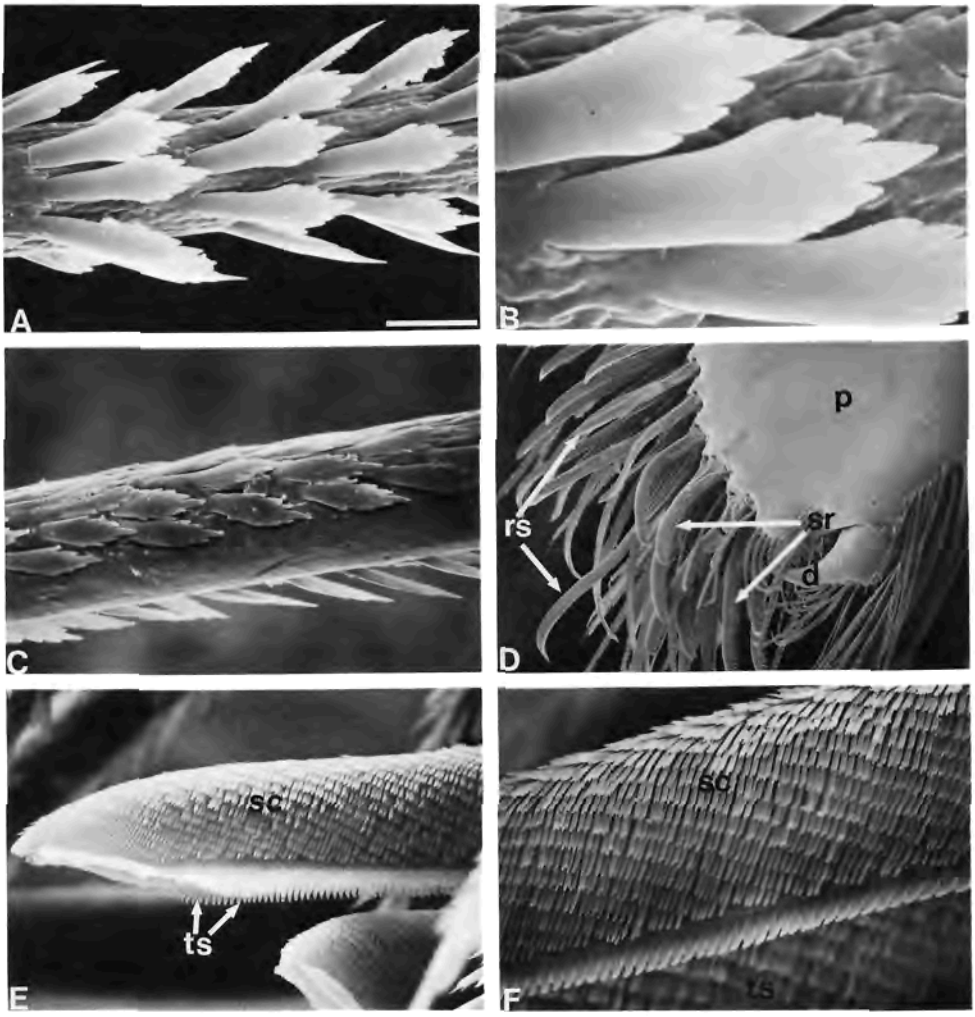

Fig. 4. *Gonodactylus oerstedii*. A. Portion of multiscaled setal shaft; scale marker = 7 μm. B. Digitate scale setules from a multiscaled seta; scale marker in A = 3 μm here. C. Portion of shaft of seta from proximal part of M1 merus, showing rudimentary development of scale setules; scale marker in A = 6 μm here. D. Tip of M1 propodus, lateral view, showing location of rasp and serrate "double comb" setae along extensor margin; d = dactylus; p = propodus; rs = rasp setae; sr = serrate setae; scale marker in A = 220 μm here. E. Distal end of rasp seta from M1 propodus; sc = area of scale setules; ts = tooth setules; scale marker in A = 13 μm here. F. Shaft of M1 rasp seta; sc = area of scale setules; ts = tooth setules; scale marker in A = 18 μm here.

of *Pseudosquilla ciliata* is shown in Fig. 6C, D. The M5 brush of this species illustrates both the relatively larger size and different setation typical of families such as the Pseudosquillidae, Squillidae, and others (see Jacques, 1983) in which the M5 brush is not composed of multiscaled setae but, instead, of rasp setae identical to those on the M1 propodus of all stomatopods.

Amputation Experiments

The general null hypothesis tested was that there would be no difference in epibiotic fouling of body parts between groups of *G. oerstedii* with and without

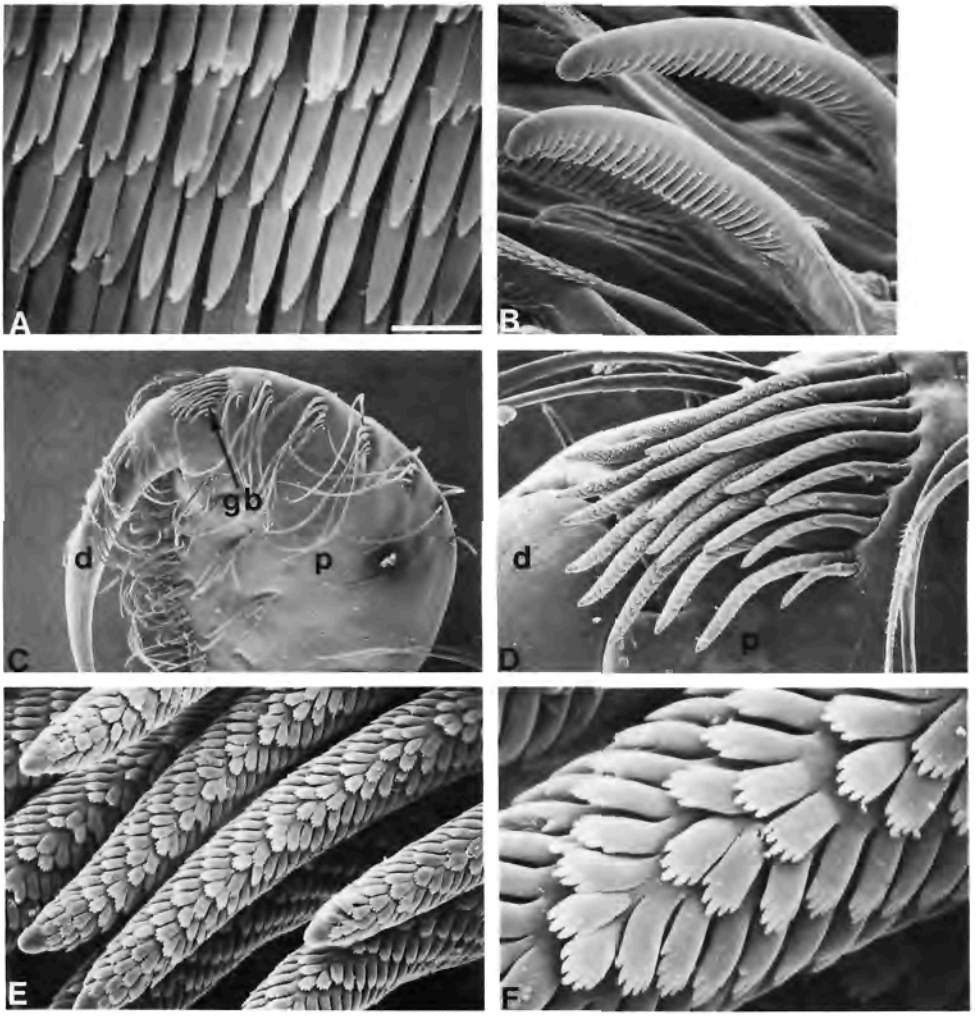

Fig. 5. *Gonodactylus oerstedii.* A. Digitate and bladelike scale setules from shaft of M1 rasp seta; scale marker = 2 μm. B. Serrate ("double comb") setae from distosuperior margin of M1 propodus (see Fig. 4D for location); scale marker in A = 56 μm here. C. Medial view of fifth maxilliped (M5) propodus and dactylus, showing vestigial grooming brush; d = dactylus; gb = grooming brush; p = propodus; scale marker in A = 500 μm here. D. Grooming brush on M5 propodus; d = dactylus; p = propodus; scale marker in A = 87 μm here. E. Multiscaled setae from M5 grooming brush shown in C and D; scale marker in A = 18 μm here. F. Portion of shaft of a multiscaled seta from the M5 propodal brush setae shown in E; scale marker in A = 5 μm here.

the first maxillipeds, appendages observed to brush and scrape many parts of the exoskeleton. The experimental group in the "Light" and "Dark" experiments had the first maxillipeds amputated, and the control groups suffered similar trauma with the amputation of part of the third pereiopods. In the analysis of experiments, counts of *Leucothrix,* a filamentous long-chained bacterium, were used to compare fouling on body parts (aesthetascs of one antennule, one eye, a gill filament) between groups. A subjective scale was employed in measurement of uropod fouling. Molting would have eliminated or reduced the potential amount of fouling in these experiments. However, only one stomatopod molted after the first day

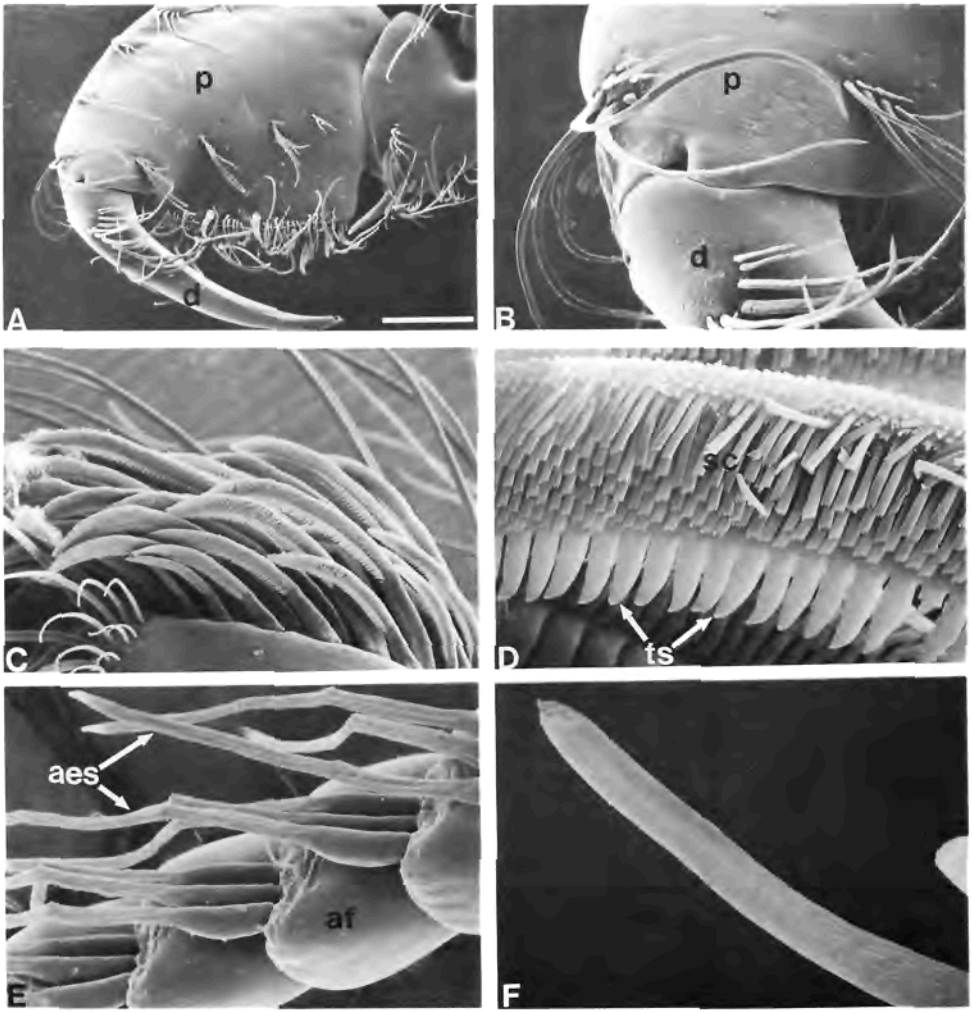

Fig. 6. *Gonodactylus oerstedii,* A, B. A. Medial view of fourth maxilliped (M4); note absence of grooming brush near propodal-dactylar articulation (compare to Fig. 5C); d = dactylus; p = propodus; scale marker = 513 μm. B. M4 propodal-dactylar articular area; note absence of grooming setae (compare to Fig. 5D); d = dactylus; p = propodus; scale marker in A = 167 μm here. *Pseudosquilla ciliata,* C, D. C. M5 propodal grooming brush of rasp setae; scale marker in A = 125 μm here. D. Shaft of rasp seta from M5 grooming brush; sc = area of scale setules; ts = tooth setules; scale marker in A = 12 μm here. *Gonodactylus oerstedii,* E, F. E. Portion of antennular (A1) flagellum of a "control" (grooming) individual from an amputation experiment; note absence of fouling on aesthetascs (compare to Fig. 7A,D); aes = aesthetascs; af = A1 flagellar segment; scale marker in A = 48 μm here. F. Single aesthetasc from A1 flagellum of a "control" (grooming) individual from an amputation experiment; note absence of fouling (compare to Fig. 7B, C, E, F); scale marker in A = 14 μm here.

during experiments, and data from this individual is not included in the data analysis below.

Fouling by *Leucothrix* and other microbial organisms was heavy on the antennular aesthetascs (Fig. 7A–F) of the experimental group in both experiments, while those of the control groups remained clean (Fig. 6E, F). Aesthetascs from nongrooming animals were covered with long strands of *Leucothrix,* budding

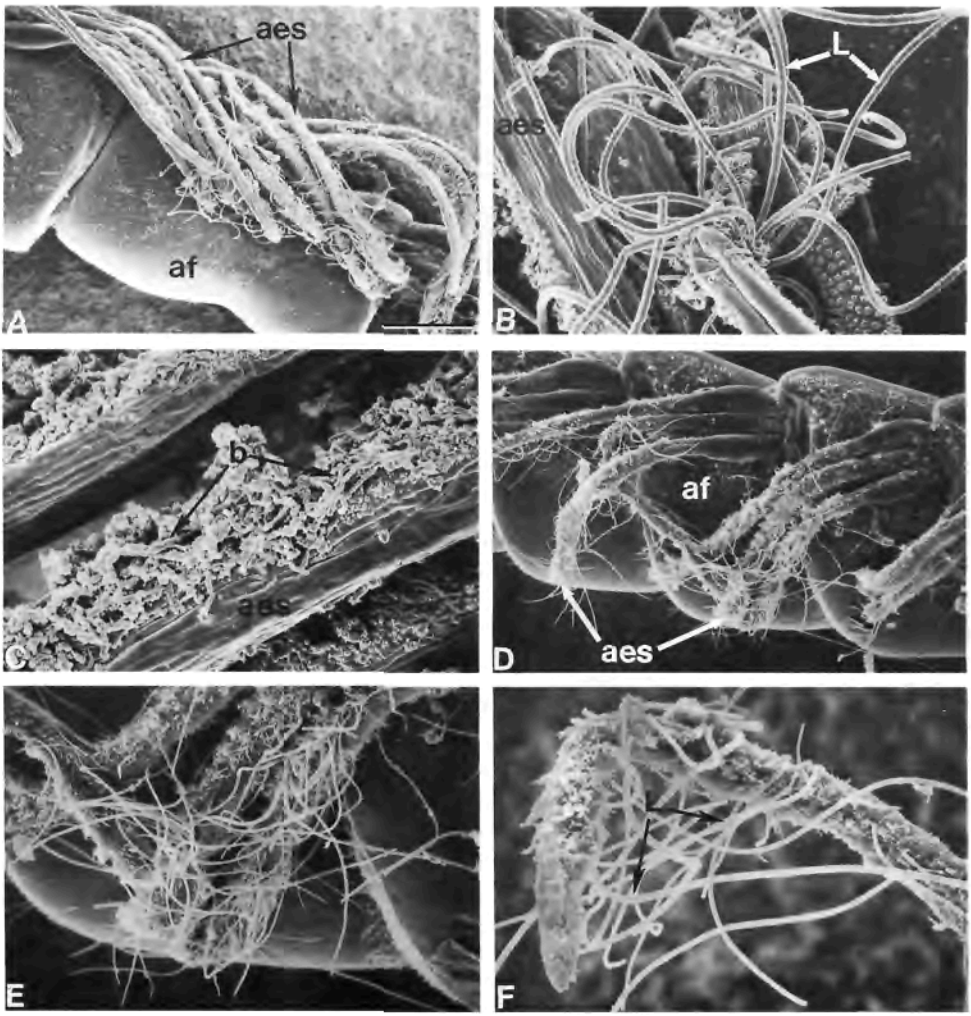

Fig. 7. *Gonodactylus oerstedii.* A. Portion of A1 flagellum from "experimental" (nongrooming) individual from "Dark" amputation experiment; note microbial fouling on aesthetascs (compare to Fig. 6E); aes = aesthetascs (arrows); af = A1 flagellar segment; scale marker = 56 μm. B. Fouled aesthetascs from A; note long strands of bacterium *Leucothrix* (compare to Fig. 6F); aes = aesthetasc surface; L = *Leucothrix* (arrows); scale marker in A = 10 μm here. C. Aesthetascs from same individual as in A, showing mixture of bacteria and bacterial exudates on aesthetasc surface (compare to Fig. 6F); aes = aesthetasc surface; b = bacteria and exudates (arrows); scale marker in A = 6 μm here. D. Portion of A1 flagellum from "experimental" individual from "Light" experiment; note fouling on aesthetascs and nearby surfaces (compare to Fig. 6E); aes = aesthetascs (arrows); af = A1 flagellar segment; scale marker in A = 71 μm here. E. Group of fouled aesthetascs from D; note coating of microbial fouling (compare Fig. 6E); scale marker in A = 29 μm. F. Single fouled aesthetasc from same individual as in D; note *Leucothrix* and other microbial fouling; L = *Leucothrix* (arrows); scale marker in A = 15 μm here.

colonies of *Leucothrix,* organic debris, and an apparent mixture of various bacteria and bacterial slime (compare to microbial fouling of crustaceans illustrated in Sieburth, 1975, and Bauer, 1977, 1979).

Counts of filaments of *Leucothrix* on aesthetascs were used to quantify fouling (Table 2). Strands of *Leucothrix* were abundant on the antennular aesthetascs of

Table 2. Fouling by *Leucothrix* on experimental (nongrooming) and control (grooming) *Gonodactylus oerstedii* in the first maxilliped amputation experiments. For each treatment, the median and the range (in parentheses) of the number of filaments of *Leucothrix* on a body part are given. Number of individuals in each treatment: "Dark" experimental, 10; "Dark" control, 8; "Light" experimental, 4; "Light" control, 7.

Body part	Experimental treatment	Control treatment
Antennular aesthetascs		
"Dark" experiment	240 (86–474)	0 (0 or 1)
"Light" experiment	255 (131–578)	1.5 (0–7)
Gill filament		
"Dark" experiment	35 (6–76)	0 (0)
"Light" experiment	116 (23–220)	0 (0)
Eye		
"Dark" experiment	0 (0)	0 (0)
"Light" experiment	38 (0–142)	0 (0)

experimentals of both experiments but nearly absent from those of controls (Table 2). There was no statistical difference in medians of fouling by *Leucothrix* between the "Light" and "Dark" experimental groups (Table 2; rank sum test: $P \gg 0.20$). Microalgal fouling was expected on experimentals from the "Light" experiment. Although diatoms were found on 2 of 4 "Light" experimentals and 1 of 10 "Dark" experimentals, their number was so low (5, 7, 1, respectively) that their occurrence is not considered important.

Fouling on the gills showed a pattern similar to that on the antennular aesthestascs (Fig. 8A–D) (Table 2). Gills from experimental animals were fouled with a coating of *Leucothrix*, organic debris, and various other bacteria and bacterial exudates; gills of control individuals remained clean. Although the data indicated a possible difference between the "Dark" and "Light" experimental groups in gill fouling, the results of a rank sum test ($P > 0.10$) support the null hypothesis of no difference in median number of strands of *Leucothrix* per filament between the two groups.

Although eye scrubbing is a somewhat frequent grooming behavior in *G. oerstedii*, *Leucothrix* or other fouling did not occur on the eyes of experimentals (nor controls) of the "Dark" experiment (Table 2). However, there was some *Leucothrix*-fouling on the eyes of "Light" experimentals but none on those of "Light" controls (Table 2). A lack of statistical difference between medians of these latter treatments (rank sum test: $0.05 < P < 0.10$) is probably due to the small sample sizes involved.

The degree of fouling on individual uropods was assigned a score from 1 (no fouling) to 4 (heavy fouling). In the "Light" experiment, the median score was 2 for the experimental group and 3 for the control group. Median scores were reversed in the "Dark" experiment, i.e., 3 for the experimental group, 2 for the controls. The null hypothesis of no difference in average score between groups was tested with the rank sum test for both the "Light" and "Dark" experiments. In both cases, the null hypothesis of no difference in fouling was accepted ($P > 0.20$).

Discussion

Generalizations about the behavioral organization of crustacean grooming behavior, based on studies with decapods (Bauer, 1977, 1981, in press a) and am-

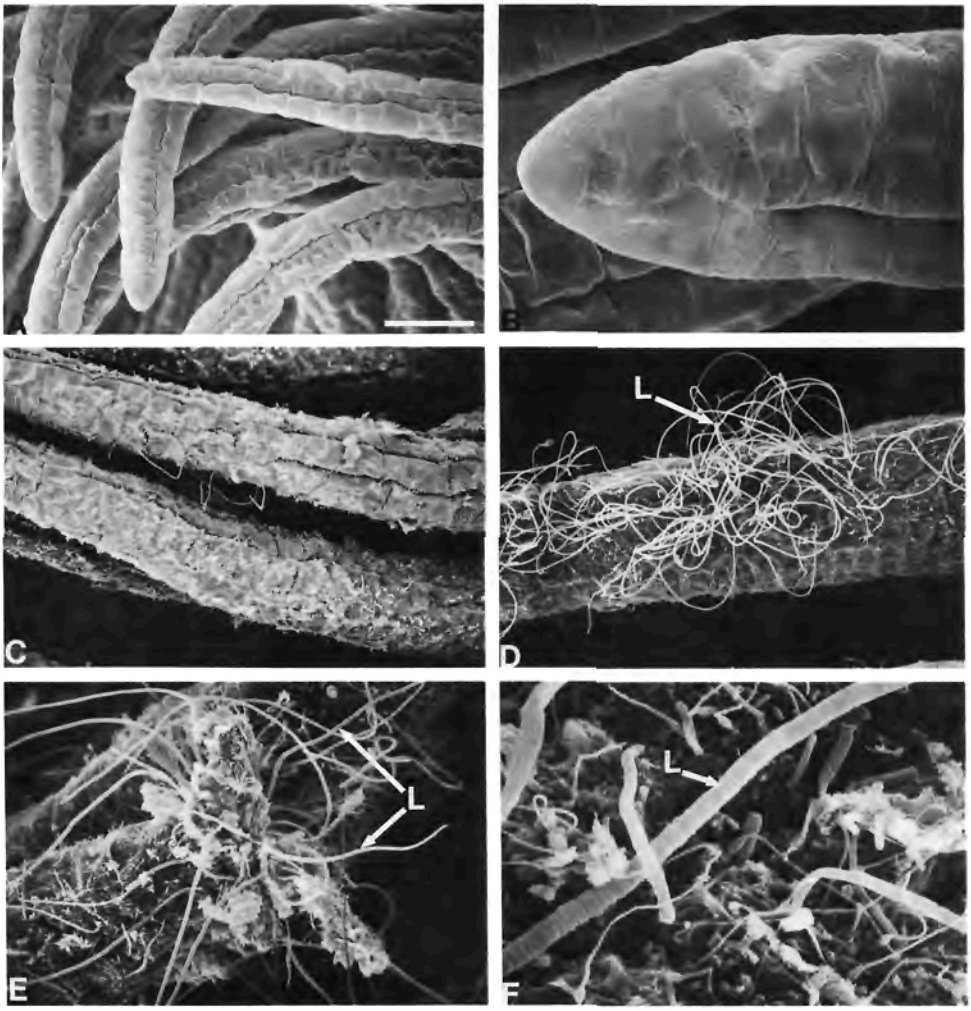

Fig. 8. *Gonodactylus oerstedii.* A. Gill filaments of a "control" (grooming) individual from an amputation experiment; note absence of fouling on filament surfaces (compare with C and D); scale marker = 140 μm. B. Tip of gill filament from same individual as A; note clean filament surface (compare with E and F); scale marker in A = 27 μm here. C. Gill filaments from "experimental" (nongrooming) individual from "Dark" amputation experiment; note coat of fouling (compare with control filaments in A); scale marker in A = 69 μm. D. Gill filament of "experimental" individual from "Light" experiment; note heavy fouling by *Leucothrix* (arrow); L = *Leucothrix*; scale marker in A = 54 μm here. E. Microbial fouling on gill filament from same individual as D; L = *Leucothrix* (arrows); scale marker in A = 28 μm. F. Microbial fouling on gill filament; note large filament of *Leucothrix,* budding colonies of *Leucothrix,* and other fouling; L = *Leucothrix* (arrow); scale marker in A = 5 μm here.

phipods (Holmquist, 1985), also apply to the stomatopods *Gonodactylus oerstedii* (this study) and *Squilla mantis* (Morin *et al.,* 1985). Preening of the antennae (A1 and A2) is the most frequent grooming behavior in *G. oerstedii,* and most other cleaning involves the cephalothoracic region (eyes, other maxillipeds, areas below the carapace). Cleaning of abdominal areas is rarer and, in *G. oerstedii,* mainly directed at the gills. Morin *et al.* (1985) have shown that there is a mainly anterior-posterior gradient in grooming effort in *S. mantis.*

Another generalization about grooming that applies to *G. oerstedii* is that there is an inverse relationship between the frequency and duration of grooming bouts. More frequently performed bouts of cleaning behaviors, such as antennae preening or eye scrubbing, are stereotyped and rapid, usually less than one second in duration. Gill preening is rarely performed, but, when it occurs, has a longer bout duration. Morin *et al.* (1985) have reported a similar relationship in *Squilla mantis*. Bauer (1977; in press a) has suggested that frequent grooming of antennules, antennae, and other cephalothoracic appendages and structures occurs because sensory receptors (chemical, tactile, visual) are numerous and must be kept free of even short-term fouling. Morin *et al.* (1985) suggest that frequent grooming also may prevent saturation and fatigue of receptors by environmental stimuli. The most infrequent grooming behaviors, gill and general body grooming in *G. oerstedii* and abdominal grooming in *S. mantis* (Morin *et al.*, 1985), have the longest bout duration. When the gills are groomed, the first maxillipeds must reach and clean numerous filaments of complex topography, a more time-consuming procedure than the quick brush of an antennule. Gill grooming can be infrequent because short-term fouling on these nonsensory structures might not interfere seriously with gas exchange. However, Morin *et al.* (1985) recorded an infrequent but long duration preening of a chemoreceptive area on the abdomen of *S. mantis;* the function of this grooming was probably to prevent fatigue of sensory receptors.

The total time and energy that *G. oerstedii* devotes to grooming is quite low when compared to *S. mantis* and to some decapod crustaceans. The median of total time spent in grooming was 1% in *G. oerstedii* compared to 36% in *S. mantis* (Morin *et al.*, 1985). In the caridean shrimp *Heptacarpus pictus,* 70% of total activity was devoted to grooming (Bauer, 1977). Stomatopods have a low diversity of numbers and kinds of grooming appendages in comparison with decapod crustaceans. In decapod species, brushes, combs, and other grooming structures may be present on several of the cephalothoracic appendages (Bauer, 1981, in press a). In the Stomatopoda, the setal brushes on the carpus and propodus of the first maxillipeds (M1) are the major grooming structures (Kunze, 1981). An apparent accessory grooming brush is located on the fifth maxillipeds in most stomatopod groups (Kunze, 1981; Jacques, 1983). One probable explanation for the low diversity of stomatopod grooming structures is the general conservativeness of the overall stomatopod body plan. A much greater number of body plans (natant, macruran, anomuran, brachyuran) occur in the Decapoda, and a greater number and variety of grooming appendages and structures has evolved to clean these various morphologies. However, the diversity of *setal types* on the fewer grooming appendages that stomatopods possess may equal the total setal diversity of the more numerous grooming structures of a given decapod species. In other words, stomatopods may be as well equipped overall to groom the body surfaces as are decapods.

In *G. oerstedii,* three major setal types are adapted for and used in grooming. The scaled serrate setae, set in rows on the M1 carpus, are used in antennular grooming. These setae are nearly identical in microstructure to aesthetasc cleaning setae on the third maxillipeds of decapod crustaceans (Bauer, in press a). Long multiscaled setae, principally on the distal and inferior borders of the M1 carpus in *G. oerstedii,* are very similar in microstructure to multiscaled setae found on structures (chelae, setobranchs, epipods) shown or believed to clean the gills in nonbrachyuran decapods (Bauer, 1979, 1981, in press a). Behavioral observations on *G. oerstedii* suggest that the multiscaled setae may be those primarily in contact with gill filaments during gill brushing. The M1 propodus of *G. oerstedii* is set

with rasp setae, a setal type unique to the Stomatopoda (Jacques, 1981, 1983). These setae appear adapted for scraping hard surfaces and may be analogous to stout serrate setae of general body-grooming brushes of decapods.

On the propodal segment of the fifth maxilliped (M5) of *G. oerstedii* is a group of compound setae whose microstructure suggests a grooming function. An M5 brush of compound setae is widespread in the Stomatopoda (Kunze, 1981; Jacques, 1983) and it is usually assumed that it is a grooming brush (Jacques, 1983). Giesbrecht (1910) reported its use in abdominal cleaning in *S. mantis*, while Kunze (1981) mentions its minor role in grooming in the squillid *Alima laevis*. I never observed the M5 brush to be used in grooming in *G. oerstedii*. Kunze (1981) suggested that the M5 brush is reduced in gonodactylids when compared to that of squillids. My observations on functional morphology of *G. oerstedii* suggest the hypothesis that the M5 propodal brush is vestigial in gonodactylids. The reduction of the M5 brush in *G. oerstedii* is perhaps a reflection of an overall reduction in grooming in gonodactylids relative to squillids. Jacques (1983) has documented that members of the gonodactyloid families Gonodactylidae, Odontodactylidae, and Protosquillidae have similar "scale" setae ("soies à écailles") in the M5 brush, whereas all other stomatopods have an M5 brush with the same rasp setae as those found on the first maxilliped. Evidence presented here suggests that the gonodactylid M5 brush is vestigial and associated with a lack of observable grooming. This information indicates that a reduced M5 brush of multiscaled setae is a derived or advanced character in the Stomatopoda, a synapomorphy of the Gonodactylidae, Odontodactylidae, and Protosquillidae. I concur with Jacques' (1983) suggestion that this character is evidence supporting close relationship among these three gonodactyloid families.

Amputation experiments resulted in microbial fouling on antennules and gills of experimental groups (M1 amputated, no grooming), while the same structures remained clean in control groups (M1 retained, presumed grooming). Fouling on antennular aesthetascs was similar to that found in amputation experiments of similar duration with decapod crustaceans (Bauer, 1977, in press a). It is likely that fouling of antennular aesthetascs, shown to be sites of distance chemoreception in many crustaceans (Ache, 1982; Gleeson, 1982), would have the same deleterious effect on perception of the environment as that proposed in decapod crustaceans (Bauer, 1977, in press a). Although preliminary qualitative observations made with light microscopy indicated little fouling on gills of experimental animals (Bauer, in press b), SEM observations and measurements of microbial fouling have shown that gill filaments of experimental *G. oerstedii* developed a coat of microbial fouling similar to that on aesthetascs. Control gill filaments remained quite clean, presumably because they were groomed by the unablated first maxillipeds. However, little or no sediment fouling occurred on gills of experimental *G. oerstedii*. In experiments with decapods (Bauer, 1979; Pohle, in press), sediment fouling was heavy on gills of animals deprived of cleaning limbs. The difference may be accounted for by the fact that stomatopod gills are not enclosed in a branchial chamber, an environment in which sediment is easily trapped by gill filaments as the respiratory stream passes by.

Fouling on the eyes, structures often groomed by *G. oerstedii*, did not develop in any of the "Dark" experimental group; however, 2 of the 4 "Light" experimental individuals had some fouling by *Leucothrix*. Eye scrubbing or grooming may not be a primary or important antifouling adaptation. Holmquist (1985) has observed and discussed possible displacement grooming in amphipods and other crustaceans. Eye grooming might be a displacement behavior in stomatopods, a group in which complex behavioral interactions occur.

Uropodal setae of both experimentals and controls were fouled in both experiments. Particulate fouling apparently takes place as the uropod tips are dragged along the substratum, and microbial fouling flourishes among sediment and detrital particles. The lack of difference between experimentals and controls in fouling of uropodal setae indicates that little or no effort is put into cleaning these structures by *G. oerstedii*.

One unexpected result was the lack of algal fouling in the "Light" experiment. A film of green microalgal filaments developed inside the stomatopod containers in this experiment but not on aesthetascs, gill filaments, or any other body parts of the experimental group. There was no significant qualitative or quantitative difference in gill and aesthetasc fouling between the "Light" and "Dark" experimental groups. In experiments with caridean shrimps, fouling on body parts (including heavy diatom fouling) was indistinguishable from fouling on inanimate substrates placed in the vicinity of the experiment (Bauer, 1975, 1977, 1978, 1979; Felgenhauer and Schram, 1978). However, the number of experimental individuals in the "Light" experiment in the present study was small; perhaps definite conclusions on microalgal fouling of nongroomed stomatopod body surfaces are not warranted until further experiments are conducted.

Except for the antennules and gills, as noted above, there was relatively little fouling on the exoskeleton as a result of these experiments. One possible explanation might be that fouling pressure might have been low in the vicinity of the experiment. However, it has been noted that microalgal fouling was heavy in the "Light" experiment inside stomatopod containers. Additionally, a film of sediment carried in by the sea-water system accumulated on the water table and within chambers. Another possibility is that the grooming function of the first maxillipeds was taken over in the experimental group by some other appendage. However, no compensatory grooming by other appendages was observed in members of the experimental groups.

A hypothesis that should be explored in future studies is that, in addition to mechanical cleaning, another antifouling mechanism has evolved in *G. oerstedii* and possibly other gonodactylids. Bauer (1981, in press a) has suggested that those decapods that lack general body cleaning, but that nonetheless have consistently clean cuticles, might be secreting antifouling chemicals onto the surface of the exoskeleton. Both time spent in grooming and grooming morphology (M5 brush) are reduced in *G. oerstedii* relative to other stomatopods such as *Squilla mantis*. *Gonodactylus oerstedii*, like other gonodactylids, retains the well-developed grooming structures on the first maxillipeds particularly necessary for cleaning of the antennular aesthetascs and gills. These latter structures are apparently not protected by antifouling compounds, if such compounds exist. Decapods whose exoskeletons remain clean in the absence of grooming nonetheless always have antennular and gill cleaning mechanisms (Bauer, in press a).

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