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Grooming structure and function in some terrestrial Crustacea

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ABSTRACT

The terrestrial environment, with a unique set of fouling parameters, has been invaded by certain amphipod, isopod, and decapod species. In an effort to characterize grooming in these crustaceans, behavior of representative organisms was recorded, and grooming appendages were examined with light and scanning electron microscopy. The mouthparts and gnathopods, particularly the scale-bearing second pair, were the primary amphipod grooming appendages. Isopods most frequently used the mouthparts and first pereiopods for grooming, but all pereiopods performed some acts. The mouthparts were armed with both scales and setae, whereas the first pereiopods made use of a seta-lined carpal groove and the setose proximal propodus. Hermit crabs used specialized setae on the third maxillipedes and fifth pereiopods for most grooming but used the unmodified first, second, and third pereiopods as well. Most brachyuran grooming was performed with modified setae on the third maxillipedal palps and epipods, with a row of simple setae on each chelipede merus, and with the chelipede fingers. The unspecialized walking legs rubbed each other. Terrestrial, 'semiterrestrial', and aquatic amphipods of the superfamily Talitroidea have basically similar grooming behavior but differ in morphology. Although there is a paucity of literature on aquatic isopod, hermit crab, and brachyuran grooming, particularly with regard to species taxonomically close to the terrestrial crustaceans, minor differences in grooming behavior and morphology between the two groups appear to be the rule.

1 INTRODUCTION

Only three crustacean orders have representatives that can claim a truly successful assault on the terrestrial environment: Amphipoda, Isopoda, and Decapoda. Those species that have attained some degree of success on land encounter a variety of problems. These organisms must guard against dehydration by modification of activity patterns and respiratory, excretory, and ecdysal mechanisms. Furthermore, terrestrial crustaceans have compensated structurally for the lack of a supportive medium and developed new reproductive strategies.

In addition to the above problems, terrestrial crustaceans are subject to fouling pressures rather different from those of an aquatic environment. Articular membranes may be abraded by granular matter (Koepcke & Koepcke 1953), and sensory organs are more likely to be damaged or disrupted by debris than are the receptors of marine crustaceans (Price & Holdich 1980). Land crabs are colonized by nematodes (Carson 1967), mites, *Drosophila* larvae, and copepods (literature reviewed by Bright & Hogue 1972), and their exoskeletons are degraded by certain bacteria (Iversen & Beardsley 1976). Sowbugs are fouled by amoebae, ciliates, rotifers, and nematodes (literature reviewed by Vandel 1960) and are actively parasitized by tachinid fly larvae (Bedding 1965, Sassaman & Garthwaite 1984). Beach hoppers are often infested with mites (Canaris 1962, Scurlock 1975, Kitron 1980). Nevertheless, terrestrial crustaceans are certainly under less epizoic pressure, as Bauer (1981) observes, than are their marine counterparts. In light of this unique fouling scenario, how do these animals groom, and what morphological adaptations abet this grooming behavior?

In an effort to answer this question, several terrestrial species were investigated: the leaf-litter inhabiting, cosmopolitan amphipods *Talitroides alluaudi* (4) and *Talitroides topitotum*

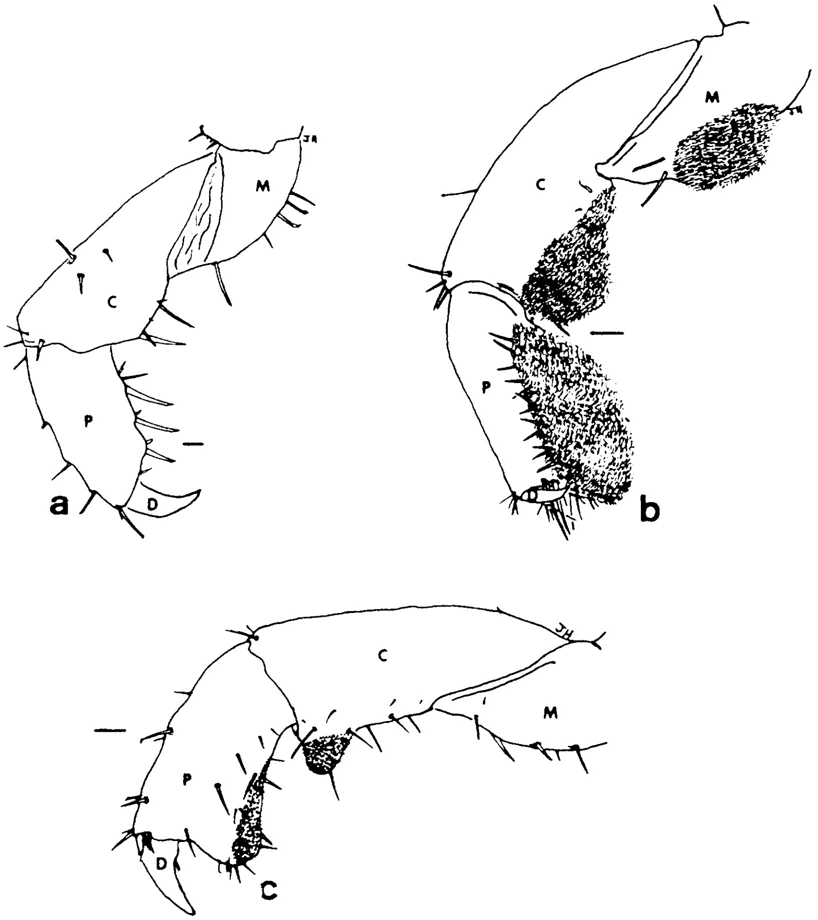

Figure 1. Representative gnathopod types. A. Simple (unguiform) first gnathopod of female *Tethorchestia* n. sp. B. Mittenlike second gnathopod of female *Talitroides topitotum*. C. Subchelate first gnathopod of male *Orchestia grillus*. Note fields of scales in B and C. C-carpus; D-dactylus; M-merus; P-propodus; bar = 50 μ (from Holmquist 1982).

(4); a conglobating isopod, *Cubaris murina* (4), and a non-conglobating isopod, *Porcellio laevis* (4); the hermit crab *Coenobita clypeatus* (4); and the land crab *Cardisoma guanhumi* (3+). (The numbers in parentheses refer to the organisms' positions on Powers & Bliss's (1983) scale of terrestrial adaptation, with a '5' indicating a very high degree of terrestriality (some even xeric) and a '1' a low degree (midlittoral).) The ensuing material on *C.murina*, *P.laevis*, *C.clypeatus*, and *C.guanhumi* is new; the Amphipoda section summarizes and extends relevant portions of previous work (Holmquist 1981, 1982, 1985). The functional morphology of grooming in these organisms is compared with available information on comparable marine and grade 2 and 3 crustaceans.

2 MATERIALS AND METHODS

All specimens were collected from the Florida Keys by hand, with the exception of *Cardisoma*, which were taken with a PVC modification of Barnwell's (1982) Philippine crab trap. Because virtually all of their grooming movements were performed ventrally and thus hidden from dorsal view, the isopods were observed in a transparent container placed on top of the clear glass stage of an inverted dissecting microscope, thus providing a ventral view. *Coenobita clypeatus* and *Cardiosoma guanhumi* were observed in both the lab and the field. Some of the hermits were transferred to surrogate, glass shells so that movements of the fifth pereiopods could be observed. Movements were recorded with a Minolta XL 401 Super-8 movie camera and a Wild Photomakroscop M 400 in conjunction with a Wild Photoautomat MPS 55.

Morphological examinations were carried out with light and scanning electron microscopy. In preparation for SEM, dissected appendages were ultrasonically cleaned, fixed with cold 3% glutaraldehyde in 0.1 M sodium cacodylate buffer for two hours, and rinsed in buffer. They were then dehydrated in an ethanol series and critical-point dried. Specimens were coated with 60% gold/40% palladium and examined with an ISI-DS 130 or JEOL JSM-3JC scanning electron microscope.

3 AMPHIPODA

3.1 *Morphology*

The superfamily Talitroidea is unusual in that it includes representatives from a variety of markedly different habitats. The first two pairs of pereiopods, or gnathopods (Fig. 1), of marine (Hyalidae: *Parhyale hawaiensis*) and freshwater (Hyalellidae: *Hyalella azteca*) species, grade 3 beach hoppers (Talitridae: *Orchestia grillus* and *Tethorchestia* n.sp. (Bousfield, pers. comm.)), and terrestrial (grade 4) leaf litter inhabitants (Talitridae: *Talitroides alluaudi* and *T.topitotum*) were examined by Holmquist (1982), who emphasized the grooming structures of these appendages.

Unlike most talitroideans, *T.alluaudi* and *T.topitotum* are neotenic. The sexes thus have similar gnathopod structure, the males lacking the large subchelate gnathopod characteristic of many other species. The first gnathopods are simple (unguiform) and are armed with stout, but unspecialized, setae (Figs. 1A, 2A). The second gnathopods are 'mittenlike' and have pellucid lobes (Hurley 1959, 1968) on the propodus, carpus, and merus (Figs. 1B, 2B). In both *T.alluaudi* and *T.topitotum*, these lobes comprise about one-quarter of the total surface area of the four distal segments and are covered with broad expanses of bristle-like scales (Figs. 1B, 2B, C, D), which are arranged in irregular rows. The scales of *T.topitotum* (Fig. 2D) occur in smaller patches and appear to be somewhat more filiform than those of *T.alluaudi* (Fig. 2C).

Females of the sexually dimorphic *Orchestia* complex have first (Fig. 1A) and second gnathopods quite similar to those of *Talitroides*. However, unlike *Talitroides*, orchestid males have small subchelate (Fig. 1C) first gnathopods and large subchelate second gnathopods. Both sexes possess echinate fields on the various gnathopodal lobes. These fields of scales have been described from *O.gammarellus* (Charniaux-Cotton 1957), *O.cavimana*, *O.mediterranea*, *O.montagui*, *O.gammarellus*, and *Platorchestia platensis* (Graf & Sellem 1970) and from *O.grillus* and *Tethorchestia* n. sp. (Holmquist 1982). In contrast to the bristle-like scales of *Talitroides*, those of orchestids resemble small fans (Fig. 3A) with broad bases and three to eleven spinules or teeth. In orchestid females, these fan-like or radiate scales make up echinate fields on the propodus, carpus, and merus of the second gnathopod, as in *Talitroides*. The first gnathopod is simple (Fig. 1A). However, the male's large second gnathopod has no radiate scales, which are instead borne by propodal and carpal lobes on the first gnathopod (Fig. 1C).

As in the orchestids, the males of the aquatic *Hyalella azteca* and *Parhyale hawaiensis* have small subchelate first gnathopods and large subchelate second gnathopods. Females have four subchelate gnathopods, all of which are basically similar to the male first gnathopod. Whereas *Talitroides*, *Orchestia*, and *Tethorchestia* have broad expanses of a single scale type, the presumed grooming structures of the aquatic species are much more concentrated and are of several types. Females carry these structures on both pairs of gnathopods; gnathopod 1 alone is so armed in the male.

3.2 *Behavior*

The talitroidean species described above were also investigated with regard to grooming behavior (Holmquist 1981). *Talitroides alluaudi* was later discussed in more detail by Holmquist (1985). The mouthparts and first and second gnathopods serve as grooming appendages in all of these talitroidean species.

Talitroides alluaudi and *T.topitotum* demonstrate basically similar grooming behavior, although *T.alluaudi* has a somewhat larger and more diverse repertoire of grooming acts. Most movements are ipsi- and unilateral, although some are contra- or bilateral. Appendages are either 'scrubbed' repeatedly back and forth or 'brushed' in a proximal-to-distal direction – a unidirectional grooming movement never occurs from the tip of an appendage to the proximal end. The second gnathopod arches into a characteristic sickle-like configuration when grooming (Fig 1B), thus juxtaposing the echinate fields (Fig. 2B, C, D) on the propodus, carpus, and merus. Receptor appendages are drawn across these processses.

The long antennae are groomed by the first and/or second gnathopods. The gnathopod(s) typically move dorsally and anteriorly past the head and continue ventrally, thus tracing a semicircle and brushing the entire antenna. Alternatively, the antennae are sometimes lowered to the gnathopods for grooming. At times, the second gnathopod will brush either the reduced first antenna or the lateral head and eye in conjunction with an antenna grooming movement. The antennae are also groomed by the maxillae; a first gnathopod grasps the antennal flagellum and pulls it to the mouthparts. The gnathopod and maxillipedal palps then hold the flagellum in place while it is chewed by the maxillae.

Talitroides also expends a great deal of energy grooming pereiopods 3-7 and the uropods and does so with a variety of movements. These appendages are scrubbed or brushed by a single first or second gnathopod or by either or both pairs of gnathopods. The animal flexes its body into a 'U' shape in order to perform the majority of these acts, with the flexion increasing as the most posterior appendages are groomed. A given appendage is often groomed by the mouth and gnathopods simultaneously. For instance, the amphipod will flex the body and grasp the proximal segments of the sixth pereiopod with both pairs of gnathopods, causing the distal segments to extend to the buccal mass. The animal then straightens the body, causing the distal segments to be scraped through the mouth and the proximal segments to be brushed between the two sets of gnathopods. This type of movement often occurs repeatedly.

Less energy is devoted to grooming general body surfaces than to grooming appendages, particularly the antennae, presumably because sensory structures are more heavily concentrated on the appendages than on the rest of the body. The non-appendage body surfaces are scrubbed almost exclusively by the two sets of gnathopods. The gnathopods often must work their way dorsally between the coxal plates or epimera (two types of lateral shield-like processes) in order to reach many of the lateral body surfaces. The dorsal surfaces of these land hoppers remain virtually ungroomed. The body is flexed into a 'U' in order for the gnathopods to reach the most posterior areas. In *T.alluaudi*, but not *T.topitotum* or other investigated talitroideans, the two sixth pereiopods elevate and either alternately or synchronously scrub the anterior abdomen.

After every few acts, the gnathopods are also groomed. Each gnathopod can be scrubbed against its opposite, and the first gnathopods can be scrubbed by the second. Both pairs of gnathopods are cleaned by the mouthparts; the maxillipedes are particularly active. Thus all material gleaned from the body is eventually handled by the mouthparts. These clumps of material are 1) worked away from the mandibles and maxillae by the maxillipedes and first gnathopods until the accumulation falls away, 2) taken from the mouthparts by the first gnathopod and stuck to nearby substrate, or 3) ingested. Grooming acts occur singly more often than in combination, although up to three movements can be performed simultaneously (e.g., a first gnathopod is cleaned by the mouthparts, while a second gnathopod scrubs the fourth pereiopod and the sixth pereiopods scrub the abdomen). In both *T.alluaudi* and *T.topitotum*, the second gnathopods, equipped with scales (Figs. 1B, 2B, C, D), have a greater repertoire of grooming movements than do the first gnathopods (Fig. 2A). Because *Talitroides* is neotenic and grooming structures are distributed similarly in the male and the female, the grooming behaviors of the two sexes are similar.

In the sexually dimorphic *Orchestia* and *Tethorchestia* (grade 3), each sex demonstrates a grooming repertoire that is distinct both from that of the other sex and from that of *Talitroides*. In the orchestids, the female's second gnathopod, using the radiate scales (Fig. 3A) on the gnathopodal lobes, performs the majority of grooming movements. The female's first gnathopod (Fig. 1A) grooms as well, but does so less frequently and has a smaller repertoire of movements than does the second gnathopod of *Orchestia* and *Tethorchestia* or the comparable first gnathopod of *Talitroides*. Orchestid males, in contrast, perform all grooming acts with the first gnathopods (Fig. 1C), directing the fields of radiate scales (Fig. 3A) against appendages and other body surfaces. The large second gnathopod does not groom and is usually motionless, tucked closely beneath the body. The mouthparts are used for cleaning in both sexes. Although the male's second gnathopod does not groom, and the brunt of the male's grooming is done by the first gnathopod, *Orchestia* and *Tethorchestia* as male/female 'composites' demonstrate grooming repertoires quite similar to that of *Talitroides*.

Females of the fresh-water *Hyalella azteca* and the marine *Parhyale hawaiensis* use specialized scales and setae on both the first and second gnathopods for grooming. The male's large second gnathopod is not used in grooming; the first gnathopods, armed with the same grooming microstructures seen in the female, perform all of the male's grooming movements. As in the semi-terrestrial species, grooming in these aquatic amphipods closely resembles that of the terrestrial *Talitroides*; the males simply do not perform second gnathopod movements.

The pellucid lobes, with their echinate field of scales, are prominent features of the investigated grade 3 and 4 amphipods. MacIntyre (1954) and Duncan (1981) noted that the lobes are used to comb the oöstegites and eggs, whereas Hurley (1959) hypothesized a 'tactile sensory function.' Graf & Sellem (1970) have variously suggested that the fields of scales are an adaptation for grooming or feeding or, drawing from permeability experiments by Graf & Magniez (1969), that they might have a physiological function such as respiration. Morino (1981) observed females scraping sand grains with the pellucid lobes and then holding the lobes up to brooded young, thus presumably transferring food. On the basis of the behavioral observations in this study, it is here held that the echinate fields are grooming structures. A dual function is, of course, quite possible.

The selective advantage of large male second gnathopods (used in at least some species for agonistic behavior (Borowsky 1984)) apparently outweighs that of a second pair of grooming appendages for semi-terrestrial and aquatic talitroideans. An obvious parallel is the display chelipede of male fiddler crabs, which cannot be used for food gathering. Aside from the

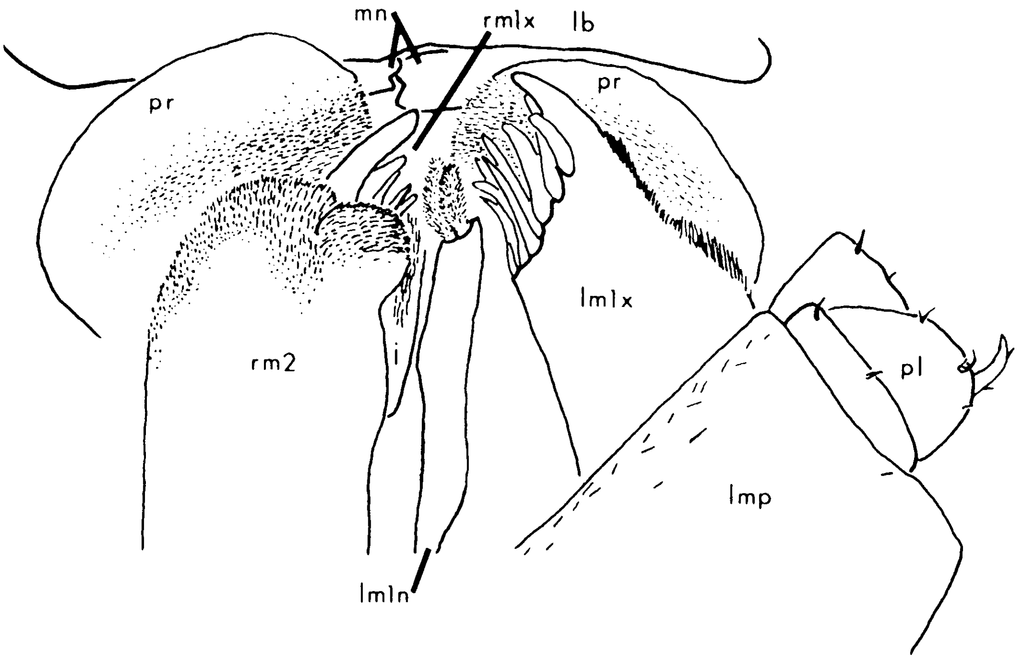

Figure 4. Distal buccal area of *Cubaris murina* (ventral view). Note scales of right maxilla and paragnaths and small disto-lateral setae of left maxillule exopod. j-junction of paragnaths; lb-labrum; lmln-left maxillule endopod; lmlx-left maxillule exopod; lmp-left maxillipede; mn-mandibles; pl-maxillipedal palp; pr-paragnath; rmlx-stout spines and setae of largely obscured right maxillule exopod; rm2-right maxilla; × 141.

grooming actions of the male second gnathopods, stemming directly from the neoteny of *Talitroides*, the behavior of land hoppers differs little from that of their semi-terrestrial and aquatic relatives. Behavioral solutions to aquatic epizoite growth may also have proven to be adequate responses to the new fouling pressures encountered as talitroideans invaded the wrack line and leaf litter. Morphological 'fine-tuning' might then have resulted in the different grooming microstructure observed in aquatic, semi-terrestrial, and terrestrial talitroideans.

4 ISOPODA

4.1 *Morphology*

The grooming appendages of *Porcellio laevis* and *Cubaris murina* were the mouthparts and pereiopods, particularly the first pereiopod (see below). The mouthparts (Fig. 4) of the two species are quite similar. Of particular interest to this discussion are the setae of the maxillules' exopods and scales (microtrichia) of the maxillae and paragnaths. The exopod of the maxillule (Fig. 4) bore a strong, disto-lateral spine and several spine-like setae, which projected distally and mesially. The disto-lateral margin of the exopod was armed with smaller, distally directed simple setae (Figs. 3B, 4). The distal maxillae and mesial paragnaths (Fig. 4) were thickly beset with scales (Fig. 3C) that appeared to be quite similar to the scales described by Wahrberg (1922) and Nordenstam (1933), the *aiguilles* (needles) of Cals (1972), and the 'fine setae' of Hassall (1977). The scales of *P.laevis* and *C.murina* demonstrated the type of gradation described by both Nordenstam and Cals, with proximal scales, consisting of several acute projections from a common base, yielding distally to longer, single structures without distinct basal portions. Such scales are present in a variety of terrestrial (Wahrberg, Hassall) and marine (Nordenstam, Cals) isopods.

The ventral margins of the pereiopods (Fig. 3D) were armed with the stout setae (trichia) (Fig. 3E) described by Holdich (1984). These structures were present on the merus, carpus, and propodus of each leg, excepting 1) the meri and carpi of the first, second, and third pereiopods in the male (Fig. 6A) and 2) the proximal propodus of the first pereiopod in both sexes (Figs. 3D, 6A). On the merus and carpus of the male, the stout setae were replaced by others with finger-like projections (Fig. 6A, B). Such a configuration is frequently encountered in oniscidean males (Vandel 1925, 1960, 1962, De Luca 1965). By contrast, females had particularly stout setae on the ventral merus and carpus of the first pereiopod (Fig. 3D). In both males and females, the proximal ventral propodus bore rows of small simple setae, which were directed distally (Figs. 3D, 6A, C).

Both sexes of each species had an unusual organ on the anterior surface of the first pereiopod (Fig. 6A). The structure was concave, beginning at the proximal third of the carpus and widening as it continued to its termination at the disto-ventral border. This carpal groove was densely packed with distally directed setae (Fig. 6D), the tips of which formed a slightly convergent pattern along the groove's midline (Fig. 6A). These setae ranged from slender, simple forms to apically serrate setae with lateral setules and graded from one type to the other within the groove.

An examination of the taxonomic literature indicates that first pereiopod ventral propodal organs of some type are very common in the terrestrial Isopoda. The propodal structures are often complemented with carpal grooves, as described here and by Holdich (1984) for

Porcellio scaber, or with adjacent organs on the disto-ventral carpus (Schultz 1984, Schultz & Johnson 1984).

4.2 *Behavior*

The grooming behaviors of *Porcellio laevis* and *Cubaris murina* were remarkably similar. The following account is applicable to both species; specific differences are noted.

All of the mouthparts and pereiopods functioned to varying degrees as grooming appendages. Although the mouthparts did not groom the antennae, they did devote much attention to the pereiopods. An appendage was cleaned in one of two ways. In the first method, a leg moved towards the antero-lateral buccal mass. The pereiopod was brought into contact with the disto-lateral portions of the ipsilateral mouthparts (Fig. 4), which were rapidly opening and closing. The appendage was pulled laterally and was thus scraped against the maxillipedal palp (Fig. 4), the mesially directed scales (Fig. 3C) of the maxilla and paragnath (Fig. 4), and setae of the lateral maxillule (Fig. 3B). This method was often used to clean the first pereiopod prior to an antenna rub. Alternatively, an appendage was positioned midventrally and was grasped by the maxillipedal palps (Fig. 4). Depending on the intensity of the movement, the leg was grasped only by the maxillipedal palps and maxillae or additionally by the greatly extended exopods of the maxillule (the endopods were possibly used as well) or even the mandibles (Fig. 4). At its most extreme, this act caused the carpus, propodus, and dactylus to pass between or across the heavily sclerotized mandibular processes, the stout distal spines of the maxillule, the scales of the paragnaths and maxillae, and the palps of the maxillipedes. The mouthparts either simply grasped the withdrawing pereiopod, thus scraping it, or actively worked the appendage between them. Sometimes the first and second pereiopods were cleaned simultaneously. Neighboring legs often held a pereiopod to the mouthparts for grooming (e.g., both sixth pereiopods assisted the fifth). As an isopod groomed progressively more posterior appendages, the body bent into an ever-increasing 'U' shape. This bending was even evident as the animal groomed the second pereiopod and was quite marked during grooming of the hindmost pereiopods. The first through sixth pereiopods were routinely cleaned. Only *C.murina* was observed to groom the seventh pereiopod, and this species spent more time orally grooming posterior appendages than did *P.laevis*, presumably because of its conglobating ability.

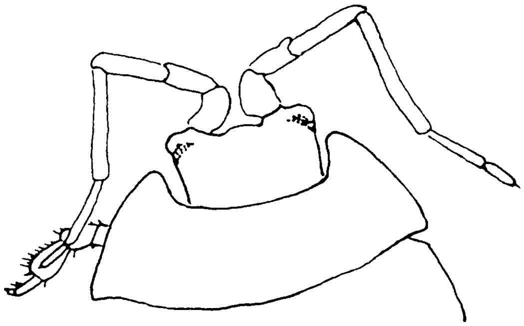

Figure 5. *Porcellio laevis* grooming antennae with first pereiopod. Pereiopod 1 has just brushed proximal antennal segments with ventral propodus and rotated, bringing carpal groove into contact with distal segments.

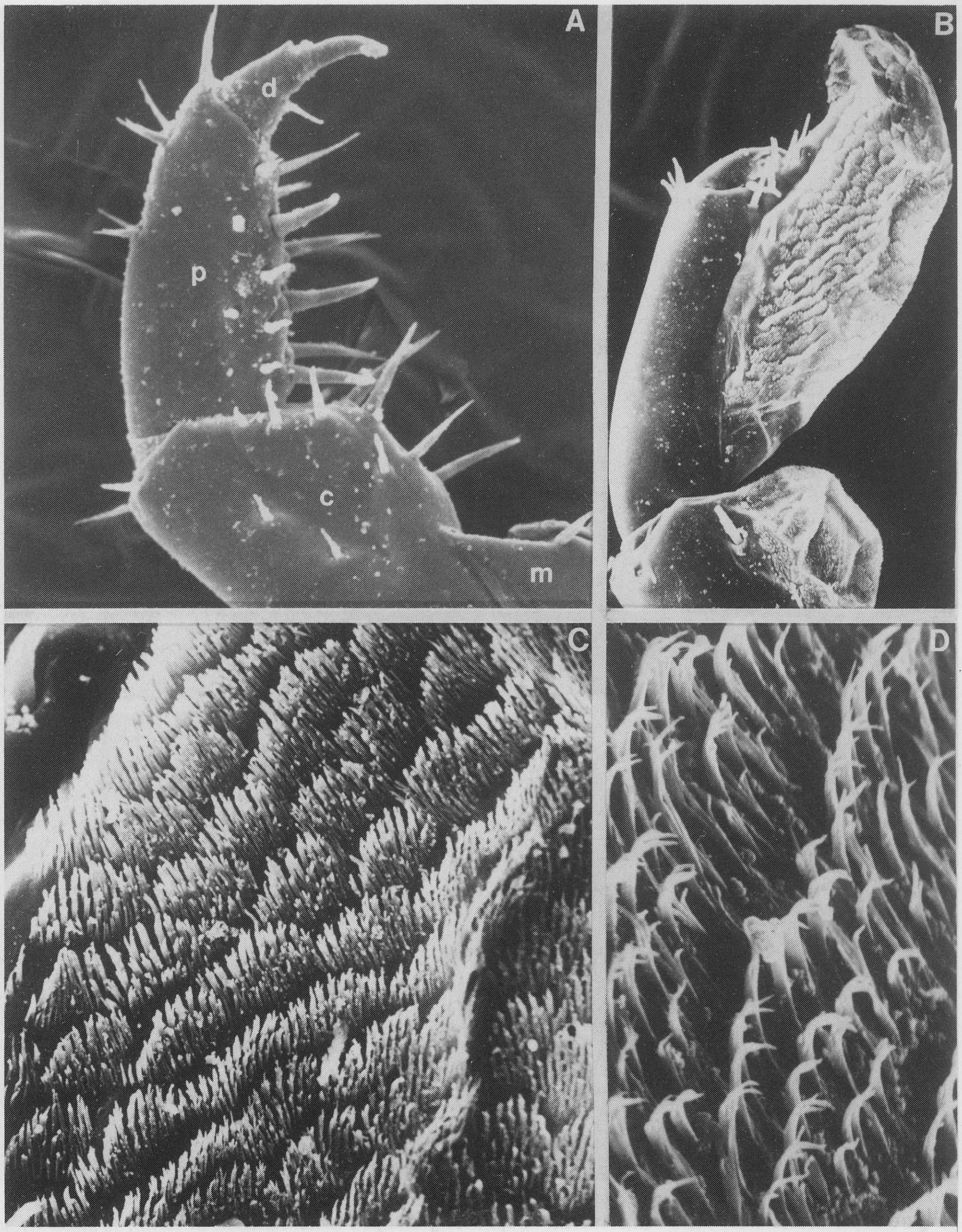

Figure 2. A. Simple first gnathopod of *Talitroides alluaudi*; c-carpus; d-dactylus; m-merus; p-propodus; × 275. B. Echinate fields on the mittenlike second gnathopod of *T.alluaudi*; × 275. C. Enlargement of propodal scales in B; × 1,200. D. Scales from second gnathopod of *T.topitotum*; × 5,060. (From Holmquist 1982.)

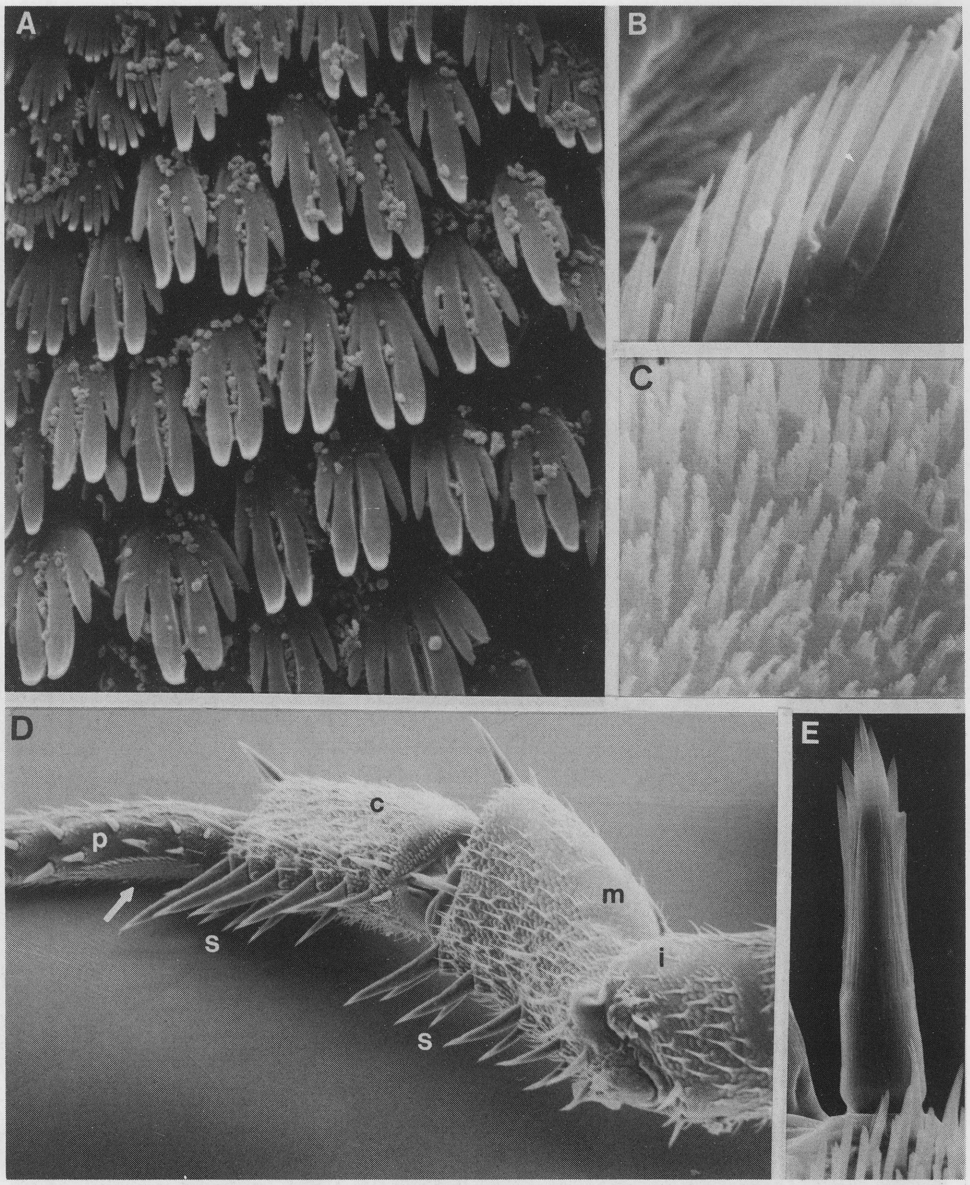

Figure 3. A. Scales from male *Tethorchestia* n. sp. first gnathopod (note variation in form); × 3,550 (from Holmquist 1982). B. Setae from distolateral exopod of *Cubaris murina* maxillule; × 1,290. C. Scales from *C.murina* distal maxilla; × 1,290. D. Posterio-ventral view of female *Porcellio laevis* first pereiopod, from propodus (p) to ischium (i); note propodal grooming organ (arrow) and stout ventral setae (s); c-carpus; m-merus; × 68. E. Stout seta from carpus of above; × 380.

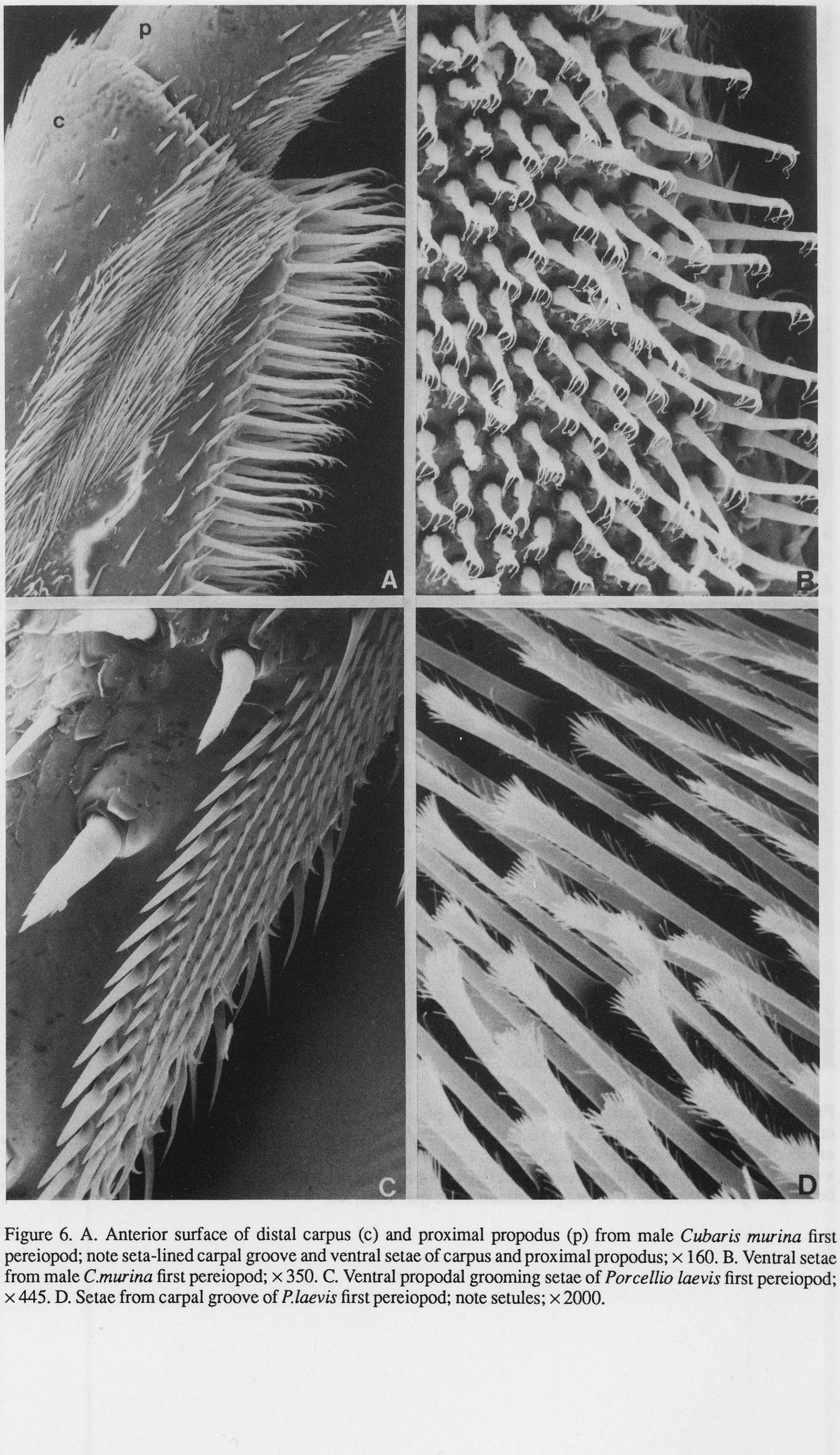

Figure 6. A. Anterior surface of distal carpus (c) and proximal propodus (p) from male *Cubaris murina* first pereiopod; note seta-lined carpal groove and ventral setae of carpus and proximal propodus; × 160. B. Ventral setae from male *C.murina* first pereiopod; × 350. C. Ventral propodal grooming setae of *Porcellio laevis* first pereiopod; × 445. D. Setae from carpal groove of *P.laevis* first pereiopod; note setules; × 2000.

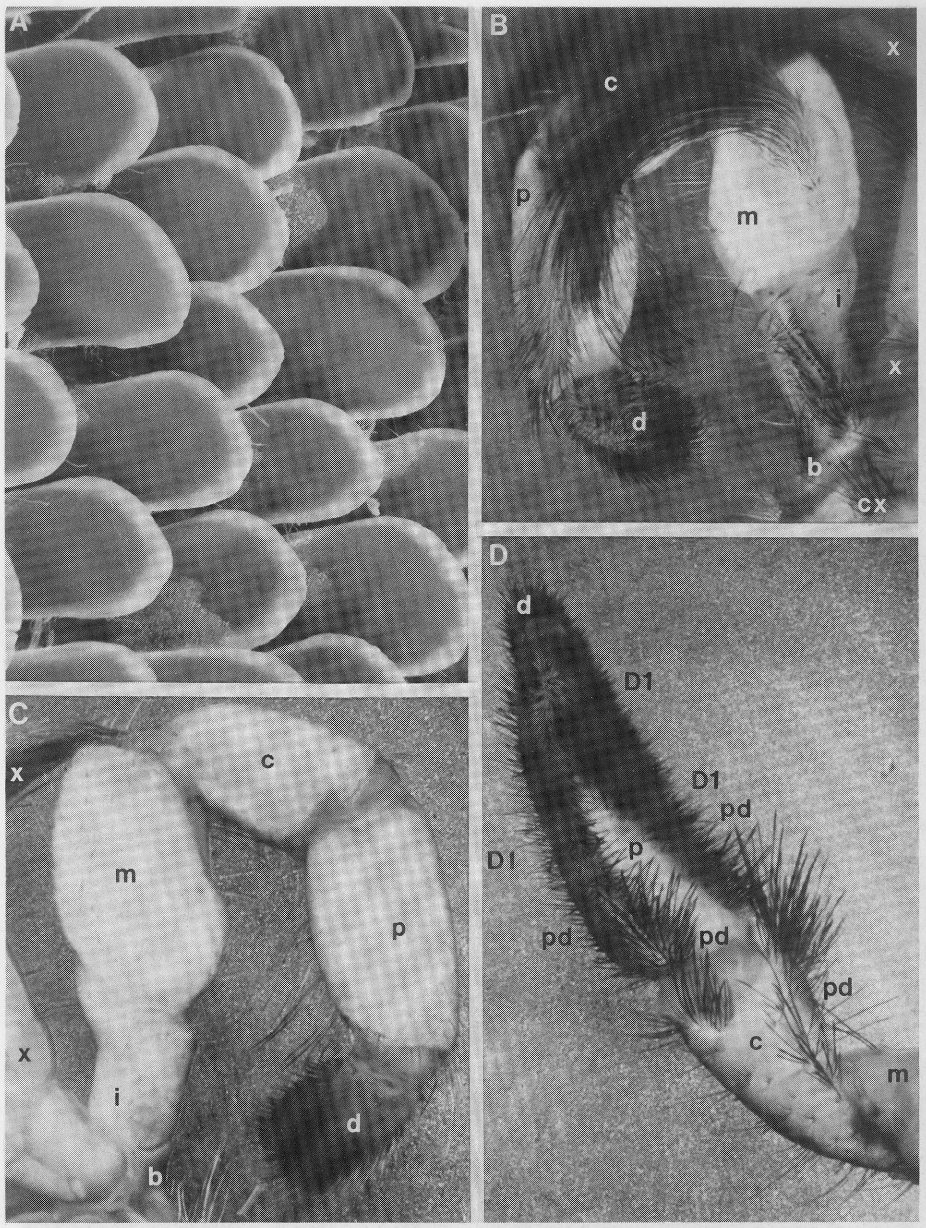

Figure 7. *Coenobita clypeatus*. A. Propodal shell-gripping scales from fifth pereiopod; × 180. B. Third maxillipede endopod (mesial view); setae of dactylus and dense meral, carpal, and propodal band are D2 serrate setae, with exception of some apical simple setae; b-basis; c-carpus; cx-coxa; d-dactylus; i-ischium; m-merus; p-propodus; x-exopod; × 6. C. Third maxillipede endopod (lateral view); × 6. D. Dorsal grooming surfaces of fifth pereiopod, bearing simple, D1 serrate (D1), and plumodenticulate (pd) setae; × 6.

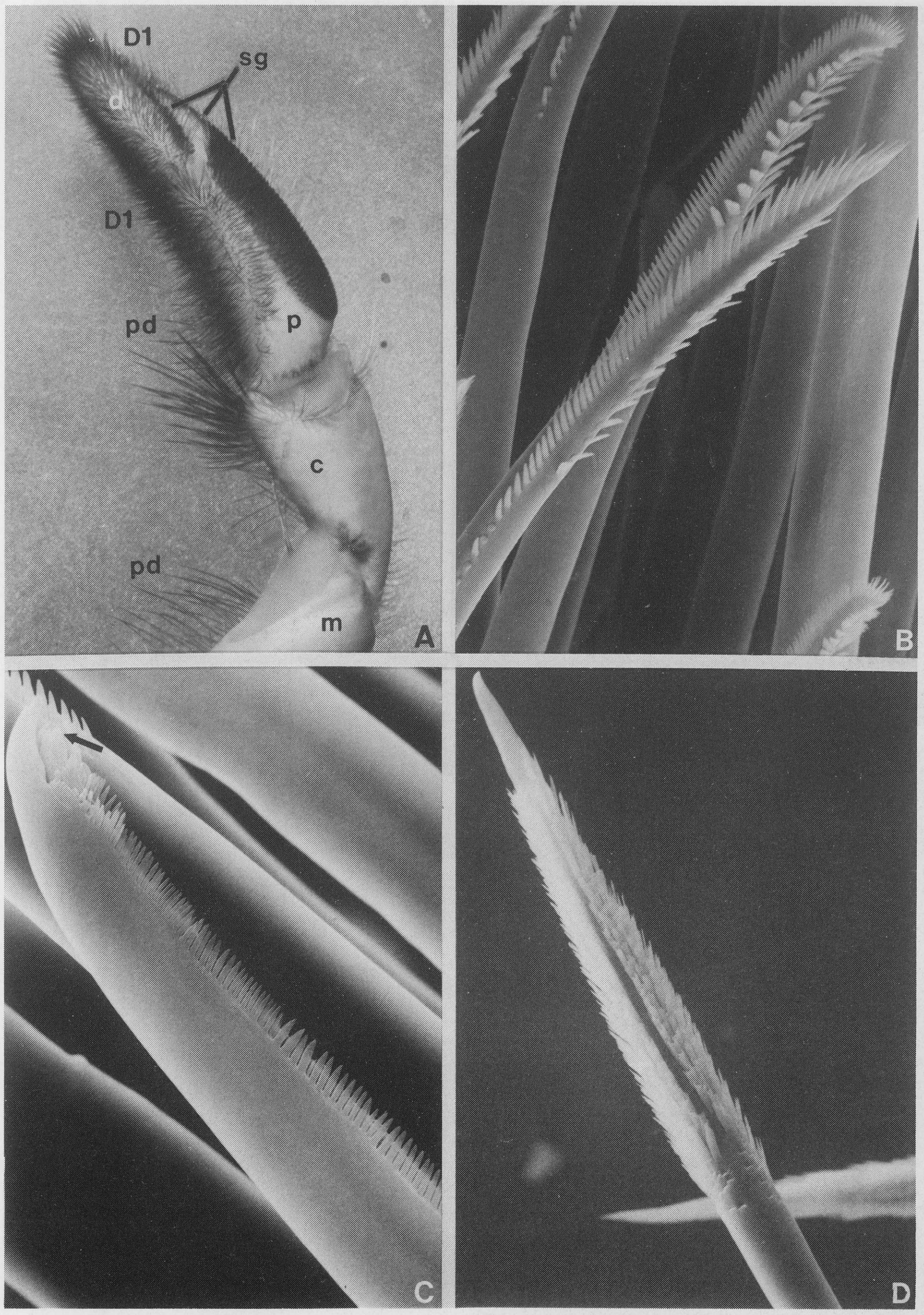

Figure 8. *Coenobita clypeatus*. A. Ventral grooming surfaces of fifth pereiopod, armed with simple, D1 serrate (D1), and plumodenticulate (pd) setae, as well as shell-gripping scales (sg); c-carpus; d-dactylus; m-merus; p-propodus; × 6. B. Type D2 serrate setae from third maxillipede propodus; note marginal serrations and central scales; × 735. C. Type D1 serrate seta from fifth pereiopod dactylus; note subapical pore (arrow); × 1,215. D. Plumodenticulate seta from fifth pereiopod propodus; × 355.

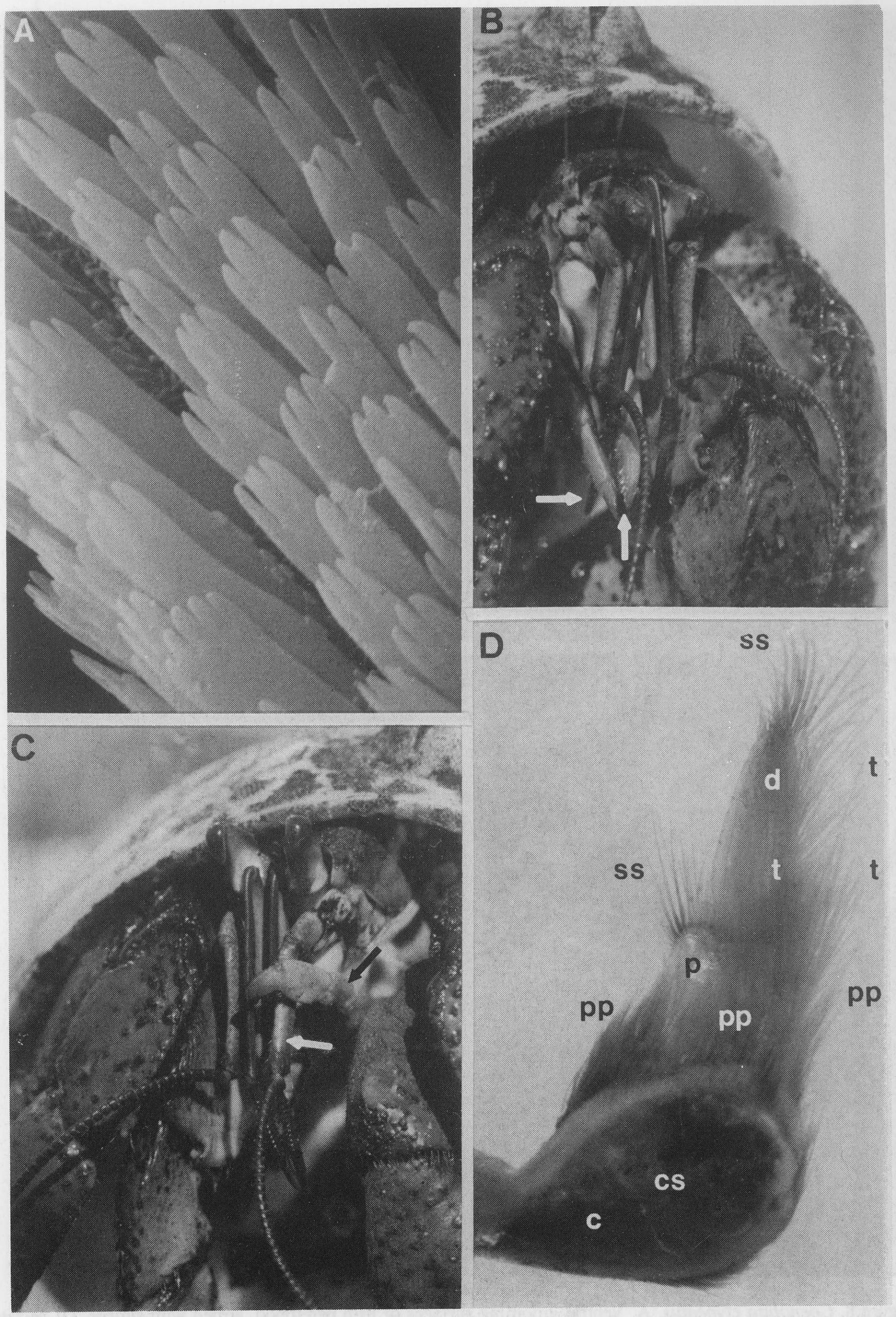

Figure 9. A. Magnification of Fig. 8D, *Coenobita clypeatus* plumodenticulate seta, showing comb-like setules and central groove; × 3,460. B. *Coenobita clypeatus* scrubbing right antennule (horizontal arrow) with both third maxillipedes (vertical arrow); × 2. C. *Coenobita clypeatus* brushing left antenna (white arrow) with left third maxillipede (black arrow); × 2. D. Inner surface of palp from *Cardisoma guanhumi* third maxillipede, with simple (ss), triserrate (t), pappose (pp), and cuspidate (cs) setae; c-carpus; d-dactylus; p-propodus; × 13.

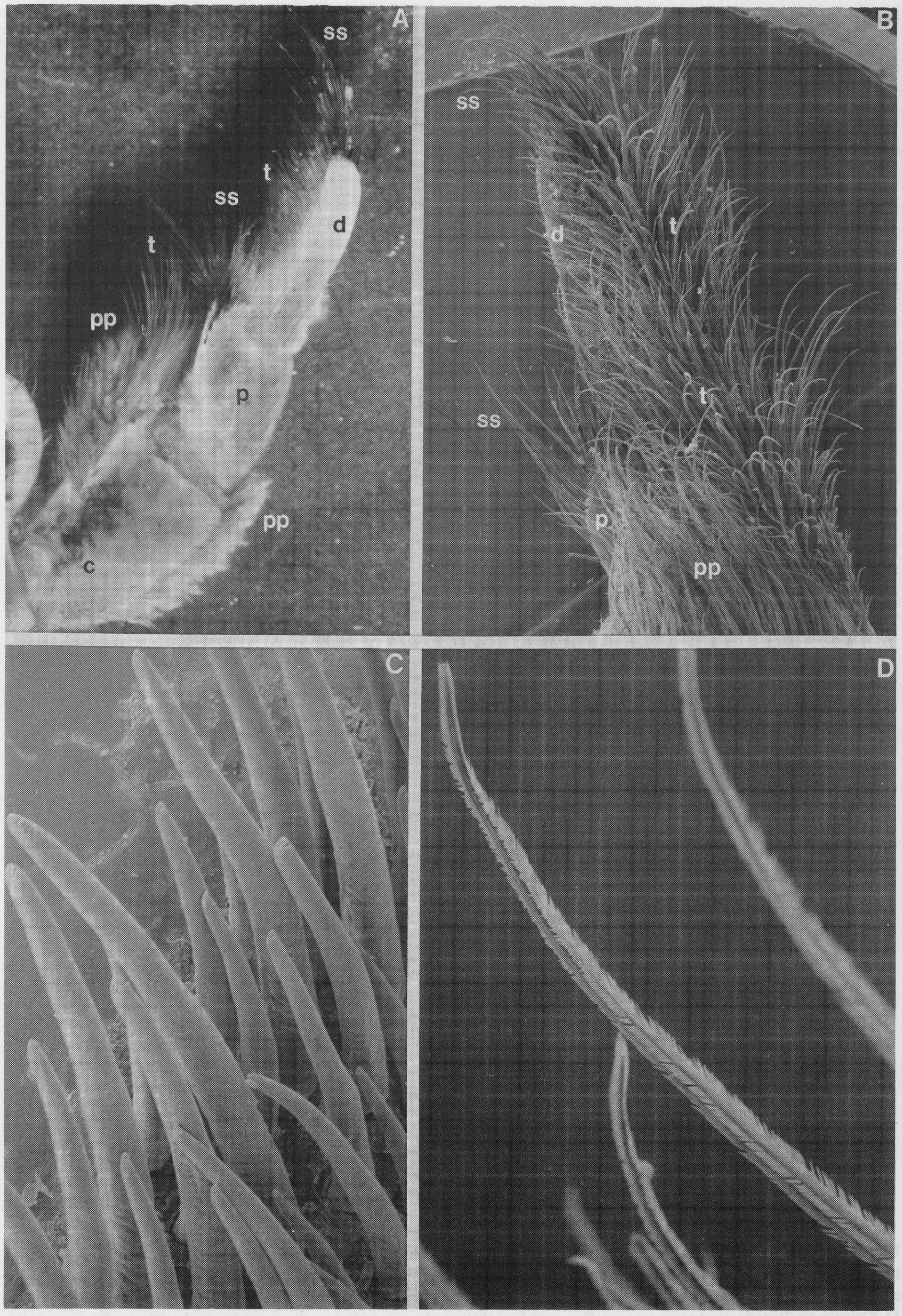

Figure 10. *Cardisoma guanhumi*. A. Outer surface of third maxillipedal palp, showing location of simple (ss), triserrate (t), and pappose (pp) setae; c-carpus; d-dactylus; p-propodus; × 9. B. Mesial edge of third maxillipede dactylus and propodus, demonstrating dense concentration of setae; × 12. C. Cuspidate setae from carpus of palp; × 130. D. Triserrate setae from propodus of palp; × 235.

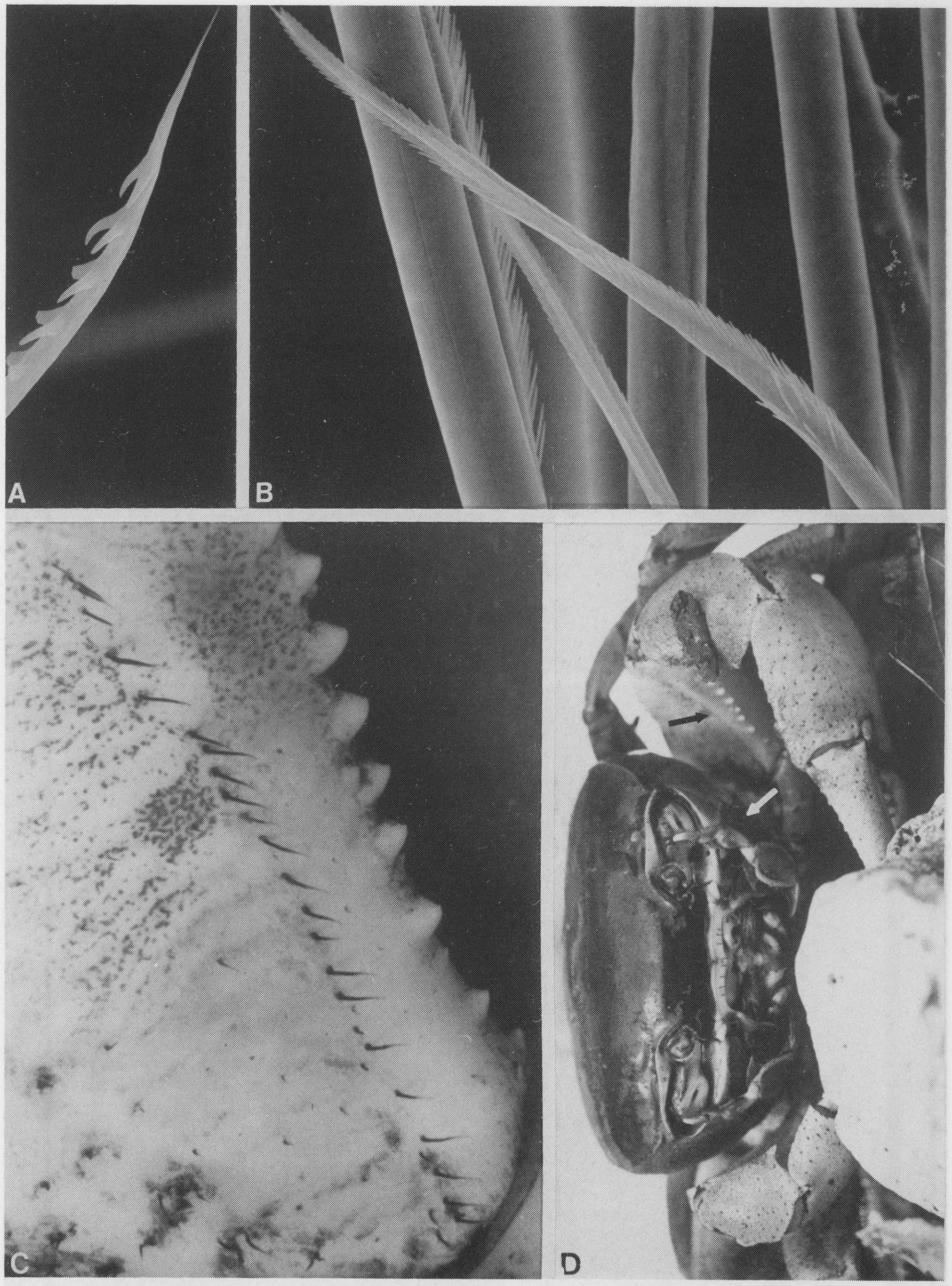

Figure 11. *Cardisoma guanhumi*. A. Distal portion of serrate seta, with stout recurved teeth, from epipod of second maxillipede; × 320. B. Serrate setae, with many fine setules, also from epipod of second maxillipede; this type far more common in *C.guanhumi*; × 465. C. Stout simple setae, on cheliped merus, used to scrub branchiostegite; × 7. D. Third maxillipedes grooming eyestalks; crab's right palp has rounded eye's posterior and will continue mesially, while left palp has progressed further; black arrow indicates position of stout setae for grooming branchiostegite (white arrow); × 0.8 (S. Sprunt).

The remaining grooming movements were all performed by the pereiopods. By far the most common of these acts was the rubbing of an antenna by the ipsilateral first leg (Fig. 5). This pereiopod was first cleaned by the mouthparts as described above. Then the antenna moved posteriorly and ventrally, where the propodus (Figs. 3D, 6A) of the first leg hooked over it at about mid-length. The propodus was then drawn laterally, scraping the dorsal surface of the antenna with its proximo-ventral setae (Fig. 6C). As the pereiopod extended from the body, the pereiopod rotated, bringing the ventro-lateral surface of the antenna into contact with the distally directed setae of the carpal groove (Figs. 5, 6A, D). This movement occurred rapidly and often repeatedly. At times, it was performed bilaterally and synchronously and occasionally without use of the carpal groove. Rarely, the second leg brushed the antenna in conjunction with the first leg. The antenna also removed offending material via a series of quick slaps against the substrate or by scraping against a leaf or soil clod.

The mouthparts were groomed by the first pereiopods, which were positioned anteriorly and then drawn posteriorly. This movement was usually bilateral and synchronous, but occasionally unilateral.

The pereiopods groomed each other in a variety of ways. The second leg crossed the first and scrubbed the latter's grooming organs. At times a pereiopod was held directly away from the body and was scrubbed between its two neighbors, which had hooked propodi over the intermediate appendage. The most common type of leg grooming was the mutual scrubbing of adjacent pereiopods, in which each simultaneously groomed and was groomed. The dactylus, propodus, and carpus were not involved in these movements. Sometimes three appendages, particularly the second, third, and fourth pereiopods, scrubbed each other. All of these acts were ipsilateral with the exception of the mutual grooming of the two seventh pereiopods. At times, the first four pereiopod pairs engaged in mutual scrubs while also being cleaned by the mouthparts. Up to three of the anterior dactyli and propodi were inserted between the mouthparts for grooming, while various neighboring pereiopods scrubbed the carpi and meri of the subject appendages.

As seen above, the grooming behaviors of *P.laevis* and *C.murina* were virtually identical, as was that of a third grade 4 species, *Porcellionides floria*, which was somewhat less rigorously observed. Reports on semi-terrestrial and aquatic isopods indicate differing approaches to the fouling problem. The grooming of the mouthparts, by the first pereiopods, of the grade 3 *Eurydice pulchra* and *E.affinis* (Jones 1968) is the same as that demonstrated by the grade 4 isopods. However, unlike the woodlice, *Eurydice* uses a setose maxillipedal palp to clean the inner mouthparts. The intertidal genus *Dynamene* possesses a long mandibular palp, which grooms the antennal flagellum (Holdich 1971). The mouthparts of the examined terrestrial species did not groom the antennae at all. The subtidal *Arcturella sawayae* uses its first pereiopods to groom a variety of surfaces, including the eyes and cephalon, and actually uses the antennae for grooming the dorsum and posterior body and pereiopods (Moreira 1973). *Cubaris murina*, *Porcellio laevis*, and *Porcellionides floria* did not groom with the antennae and did not groom the cephalon and eyes or, for that matter, any non-appendage areas. Although some of these differences are striking, it may be that they are as much due to the tremendous range of marine isopod body form as to differences in fouling pressures.

Based on the woodlouse grooming behavior presented here, it is apparent that the setae of the first pereiopod's proximal propodus (Fig. 6A, C) and carpal groove (Figs. 5, 6A, D) are important in grooming. Verhoeff (1908-09) and Wahrberg (1922) reached the same conclusion concerning similar organs on a number of woodlice. Schultz (1984) and Schultz & Johnson (1984) attributed a grooming function to structures on the proximal propodal and distal carpal margins of various terrestrial isopods. The present work demonstrates that the maxillipedal palps, scales of the maxillae and paragnaths, lateral setae of the maxillules, and sclerotized biting surfaces of the maxillules and mandibles are important grooming structures as well. The stout setae (trichia) of all seven pereiopod pairs (Fig. 3E) also have a role in grooming adjacent legs (Holdich 1984). Although the location of dense ventral stands of carpal and meral setae (Fig. 6A, B) on the first three pereiopods in the male suggests a grooming function, these organs did not perform this activity. Male sowbugs typically 'drum' or brush the anterior pereiopods against a female's dorsum during courtship behavior (Legrand 1958, Patanè 1959, Mead 1964, 1965, 1967, Sutton 1980). It seems probable that the ventral setal organs abet this behavior.

Schmalfuss (1977, 1978) has suggested that the tergal plaques (or microscales) of terrestrial isopods function primarily as passive anti-fouling devices, preventing the adherence of small wet particles. However, Powell & Halcrow (1982) observed that these plaques are not necessarily terrestrial adaptations and that their function is still unclear.

5 ANOMURA

5.1 *Morphology*

As will be seen below, *Coenobita clypeatus* used the mouthparts (particularly the third maxillipedes) and the first, second, third, and fifth pereiopods as grooming organs. The stubby, reduced fourth legs, with larger fields of shell-gripping scales (Fig. 7A) than the fifth legs, did not appear to function in grooming. Although the chelipedes and second and third pereiopods were secondary grooming appendages, they did not possess modified structures for the process. The walking legs were instead provided with the stout, simple setae described from *C.perlatus* by Hamilton (1983).

The primary grooming appendages were the third maxillipedes (Fig. 7B, C) and fifth pereiopods (Figs. 7D, 8A). The merus, carpus, propodus, and dactylus of the third maxillipedal endopod (Fig. 7B, C) were the only mouthpart segments that contacted non-oral appendages. These segments were heavily beset with Type D2 serrate setae (Fig. 8B) of Factor's (1978) classification scheme, which is followed here. These setae also appeared to be identical to those figured by Bauer (1975). Smaller numbers of Type I simple setae were also present.

The distal tip of the rounded dactylus was armed primarily with simple setae (Fig. 7B, C). The remainder was densely covered with serrate setae, although the external face was more sparsely setose (Fig. 7C). With this exception of the dactylus, the external endopod face was virtually nude (Fig.7C). Mesially, a band of setae ran from the proximal third of the merus to the distal propodus (Fig. 7B). This band was largely composed of serrate setae, with some simple setae interspersed. There was some gradation in form of the D2 serrate setae; some had an increased number of median scales, whereas others approached the C3 modified plumodenticulate setae of the exopods. All of these setae were closely applied to the maxillipede surface and were directed distally (Fig. 7B). The setae arising from the propodus were larger than those of the dactylus, with setae of the carpus and distal merus larger still. As Roberts (1968) observed for *Pagurus longicarpus* and *P.pollicaris*, the long serrate setae of the carpus overlapped those of the propodus. Setae of the distal merus, in turn, overlapped those of the carpus. The meral setae became progressively smaller and fewer in number proximally. Very sparse serrate setae occurred adjacent to the setal band. The second maxillipedes were also armed with serrate setae accompanied by scattered simple setae.

The setal complement of the fifth pereiopods was quite different from that of the maxillipedes. Type D1 serrate setae (Fig. 8C) were common and demonstrated some variation at the tips. Also present was an unusual setal type (Figs. 8D, 9A) that closely resembled Thomas's (1970) setobranch setae, although there was no mid-shaft articulation. They perhaps integrate best with Factor's (1978) scheme as C5 plumodenticulate setae, a type added to Factor's framework by Schembri (1982a, b). As with Factor's C3 plumodenticulate setae, there were no proximal setules, and the tip of the shaft was sickle-shaped as Schembri described. Type I simple setae were also present.

Most of the posterior surface of the dactylus was armed with shell-gripping scales (Figs. 7A, 8A). Ventrally and anteriorly, the dactylus was covered with serrate setae and scattered simple setae. The posterior surface of the propodus was also covered with shell-gripping scales. Otherwise, with the exception of a small mesial band of bare exoskeleton, the propodus was thickly beset with setae. Distally, these setae were primarily serrate, but plumodenticulate setae were more common proximally and became the dominant type near the carpal margin. The lateral carpus was bare except for a series of plumodenticulate setae bordering the propodus. A dense clump of long plumodenticulate setae was found on the distal ventro-mesial angle, with a somewhat smaller clump distally and dorsally. Similar, progressively smaller setal clumps occurred proximal to these groupings, with an occasional simple seta present. The lateral surface of the long merus was devoid of setae, which were present, though relatively sparse, on the dorsal, ventral, and mesial surfaces. These setae were primarily plumodenticulate distally, but serrate setae became more common proximally.

5.2 *Behavior*

The third maxillipedes and fifth pereiopods performed the majority of movements, including all of the more complex actions, and were suprisingly dexterous. *Coenobita clypeatus* devoted most of its grooming energy to the eyes and antennules and did so with the mesial surfaces of the dactylus, propodus, carpus, and distal merus of the third maxillipedal endopods (Fig. 7B). An eyestalk was groomed by one (ipsilateral) or both maxillipedes. The eyestalk dipped ventrally and was met by a third maxillipede, which hooked its dactylus over the proximal portion and applied the serrate setae of the mesial propodus and dactylus against the eyestalk. (The antennae had meanwhile swung laterally to allow access.) The maxillipede was pulled ventrally, brushing the eyestalk's full length. If both maxillipedes were used, the two dactyli were positioned together at the base of the eyestalks and were drawn ventrally in unison. The antennules may also be groomed by either (ipsilateral) or both maxillipedes. The antennules were bent upward forming an inverted 'V', while the maxillipede was raised to meet the proximal part of the appendage. The maxillipede was then pulled ventrally, brushing the antennule with its serrate setae and pulling it ventrally as well. When both maxillipedes groomed an antennule, they at times continued to grasp the flagellum at the end of the movement. The maxillipedes then scrubbed the flagellum between them (Fig. 9B), working alternately up and down as would a pair of pistons. Eye and antennule grooming movements were often combined, with the maxillipede(s) first brushing the eyestalk, then continuing ventrally to the antennule. The antennal peduncle and proximal flagellum were brushed by the ipsilateral third maxillipede (Fig. 9C). The third maxillipedes also groomed the mesial and dorsolateral surfaces of the chelipede meri and the ventral surface of the cephalothorax.

The three pairs of walking legs (chelipedes included) groomed themselves by scrubbing against each other in various combinations of two or three appendages. The dactyli, propodi, and carpi were most important in these movements. In addition, the fingers of the minor chelipede picked at the surface of the major chelipede.

The chelate fifth pereiopods were quite flexible and extended as far forward as the chelipedes. Most grooming was performed with the plumodenticulate (Fig. 8D) and serrate (Fig. 8C) setae of the carpus, propodus, and dactylus (Figs. 7D, 8A), and virtually all movements were 'scrubs'. The fingers usually opened and closed slightly when grooming; similar action has been described from the fifth pereiopods of a porcellanid crab (Bauer, this volume) and the second pereiopods of hippolytid shrimp (Bauer 1975). *Coenobita clypeatus* often extended slightly from its gastropod shell during fifth pereiopodal grooming, with the anterior abdomen thus becoming visible. The fifth pereiopods scrubbed the basal segments of the chelipedes and all of the second and third pereiopods with the exception of the dactyli. All of pereiopod 4 was scrubbed. The fifth pereiopods also groomed most of the central and posterior carapace, including the branchial chamber, and much of the abdomen. Interestingly, the shell was also thoroughly scrubbed, perhaps in an effort to rid the refuge of the green algae described by Magnus (1960) and Ball (1972). The fifth pereiopods groomed much of the shell's interior, particularly the columella and inner and outer lips, as well as the exterior lips. These appendages did not function exclusively as grooming organs, as they also use their laterally situated gripping scales (Fig. 7A) to brace the body against the shell (Johnson 1965, Vuillemin 1970).

After every few grooming acts, the fifth pereiopods moved anteriorly, in unison, to meet the two third maxillipedes, which were extended posteriorly beneath the body. The plumodenticulate and serrate setae of the posterior appendages were then scrubbed by the maxillipedes. The third maxillipedes, in turn, were scrubbed against each other and/or against the second maxillipedes after a grooming bout. The interior mouthparts had a self-cleaning function as well.

Thus, the maxillipedes groomed the anterior portion of the body (especially the sensory structures), the walking legs groomed each other, and the fifth pereiopods scrubbed the most posterior areas (Table 1). Two movements were, at times, performed simultaneously, e.g., mutual leg scrubs and antennule grooming. Although grooming may occur at any time, it was most frequent and intense immediately after a rain and was often performed in standing water if it was available. Water is clearly an important debris-flushing medium in *Sesarma* and *Cyclograpsus* (Alexander & Ewer 1969), *Uca* (Crane 1975), and *Cardisoma* (see below).

The unusual plumodenticulate setae (Fig. 8D) of the fifth pereiopods were clearly used to scrub the body surfaces. The D1 serrate setae of the fifth pereiopod (Fig. 8C) and the D2 serrate setae (Fig. 8B) of the maxillipedes were also observed to effect grooming in

Table 1. Division of labor between grooming appendages of *Coenobita clypeatus*. Groomed structures are, in order, the eyestalks, antennules, antennae, third maxillipedes, cephalothorax, pereiopods (1-5), abdomen, and shell.

Grooming appendages	Groomed structures											
	Eys	An1	An2	Mx3	Cth	Pe1	Pe2	Pe3	Pe4	Pe5	Abd	Shl
Mx3	+	+	+	+	+	+				+		
Pe1						+	+					
Pe2						+		+				
Pe3							+					
Pe5					+	+	+	+	+		+	+

C.clypeatus, as do similar serrate setae in *Pagurus* (Roberts 1968, Schembri 1982a). The maxillipedal serrate setae of a variety of marine hermits have been implicated in feeding behavior (Roberts 1968, Greenwood 1972, Kunze & Anderson 1979, Schembri 1982a); the D2 setae of *C.clypeatus* were also used for this purpose. The grooming setae, particularly the serrate setae, may also serve in a sensory capacity (Derby 1982).

Although the aesthetascs of *Coenobita* are strikingly shorter than those of its marine counterparts (Ghiradella et al. 1968a, 1968b), the terrestrial hermit's maxillipedal setae were easily as long (in terms of setal length/mouthpart length) as those found in salt-water species. Serrate setae on the distal merus of the third maxillipede, for instance, extended to the proximal third of the propodus (Fig. 7B). However, whereas the maxillipedal setae of marine hermits typically project orally and away from the flexor margin (Roberts 1968, Greenwood 1972, Caine 1975, Kunze & Anderson 1979, Schembri 1982a), those of *C.clypeatus* were very closely applied to the mouthpart surfaces. Also, the setae of the second and third maxillipede fingers of *C.clypeatus* were almost entirely D2 serrate setae, with a few scattered simple setae, instead of the wide variety of types found in marine pagurids (Kunze & Anderson 1979, Schembri 1982a). Both the acute angle of setal insertion and the homogeneity of setal types are probably adaptations to terrestrial feeding limitations rather than fouling pressures. Most aquatic hermit crabs make use of a number of feeding techniques (Boltt 1961, Roberts 1968, Greenwood 1972, Caine 1975, Kunze & Anderson 1979, Schembri 1982a). However, in the absence of a buoyant medium, filter feeding is impossible, and approaches to other processes, such as detrital feeding, may be restricted. With a reduced feeding repertoire, fewer setal types might be needed, and setal arrangements would emphasize grasping rather than straining functions. Setae projecting away from the appendage would serve little purpose and would be exposed to breakage and dehydration. An alternative may be the arrangement found in *C.clypeatus*.

The grooming behavior of *C.clypeatus* was similar in general and in most details to that described from a number of marine hermit crabs (Makarov 1962, Vuillemin 1967, Roberts 1968, Snow 1973, Field 1977, Bauer 1981, Schembri 1982a). However, some minor differences are apparent. Unlike the land hermit, *Pagurus rubricatus* grooms the second and third pereiopods with the third maxillipedes (Schembri 1982a). Field (1977) demonstrated that the third maxillipedes of *P.ochotensis* groom the antennules about 20 times as often as they do the eyes. In contrast, *C.clypeatus* groomed the eyes at least as often as the antennules. Indeed, the majority of eye and antennule grooming movements were performed in combination. It may be that the increased role of visual cues in terrestrial decapod social communication (Wright 1966, Ache 1982, Salmon & Hyatt 1983) requires, in turn, increased maintenance of the eyes.

6 BRACHYURA

6.1 *Morphology*

In *Cardisoma guanhumi*, the palps of the third maxillipede (Figs. 9D, 10A) were the most commonly used grooming structures and, like those of ocypodids (Koepcke & Koepcke 1953, Crane 1975) and grapsids (Alexander & Ewer 1969, Felgenhauer & Abele 1983), were densely setose (Fig. 10B). Four basic types of setae were apparent, and, as in the previous discussion, Factor's (1978) setal classification will be followed. The dactylus and propodus bore groups of long, Type I simple setae (Fig. 10B). Also present, primarily on the carpus, were H1 cuspidate setae (Fig. 10C). Type B2 pappose setae covered much of the palp and were interesting in that they were plumose basally, but were pappose along the remainder of the shaft. This configuration is identical to that of the pappose setae figured by Thomas (1970). Type E triserrate (Fig. 10D) setae were also inserted over much of the palps and were very similar to other Type E triserrate setae illustrated by Schembri (1982a). There was some variation of this type, with some setae resembling Type C3 plumodenticulate setae basally but becoming triserrate distally.

On the tip of the dactylus was a concentration of long simple setae (Figs. 9D, 10A, B). The inner surface of the dactylus was almost entirely covered with triserrate setae, except for the lateral edge, which was virtually devoid of setae. Conversely, only the mesial edge of the outer dactylar surface bore setae – a thin margin of triserrate and pappose types. The disto-lateral edge of the propodus was fringed with long simple setae, whereas the mesial edge was armed with a dense setal brush, predominantly triserrate distally, but increasingly pappose proximally. The carpus was fringed with dense pappose setae extending from near the base of the lateral edge, to the inner and outer faces of the propodal margin, and around to the midpoint of the mesial edge. Cuspidate setae were present among the pappose setae of the inner distal fringe and also formed a series running the length of the inner carpus.

As with other brachyurans (Borradaile 1922, Vuillemin 1967, Warner 1977, Bauer 1981, this volume), the setose maxillipedal epipods of *C.guanhumi* extended well into the gill chamber, with the first epipod above and the second and third epipods below the gills. Curious Type D1 serrate setae, similar to those described by Walker (1974) and Bauer (this volume), with stout, recurved teeth and finely tapering tips (Fig. 11A), were present. The setae of *C.guanhumi* had two rows of teeth versus a single row in the portunid *Cronius tumidulus* (Bauer, this volume). However, other Type D1 serrate setae (Fig. 11B) predominated on the epipods of *C.guanhumi*. These setae had many smaller apically directed teeth that continued to the tip of the shaft. A few scattered setules were often present at the base of the serrated portion. About 10 to 15 of these setae occurred for each of the former type.

Although the four pairs of walking legs were used for grooming, they did not appear to possess specialized grooming structures. Neither do the distal chelipede segments bear the tuberculate ridges of *Sesarma catenata* and *Cyclograpsus punctatus* (Alexander & Ewer 1969) or the serrations and setae of many fiddlers (Crane 1975) used for grooming in these latter crabs. However, the chelipede merus and ischium bore a row of stout, simple setae (Fig. 11C). The majority of these setae arose from the merus, which was concave (excepting on the adult male major chelipede), thus fitting against the convex branchiostegal region (Fig. 11D). The major chelipede merus of the mature male was long and straight, and setae were restricted to the ischium and proximal merus. The inner chelipede surfaces of a number of *Sesarma* species are armed with serrate, instead of simple, setae (Milne Edwards 1873, Felgenhauer & Abele 1983).

6.2 *Behavior*

Cardisoma guanhumi used all five pairs of pereiopods and the mouthparts (primarily the third maxillipedes) to groom its body. The most frequently performed movement was the grooming of the eyestalk and interorbital area by the third maxillipedes (Fig. 11D). Prior to grooming, the eyestalk was deflected ventrally, sometimes into its orbit. The maxillipedal palp extended dorsally, the entire maxillipede swung laterally, and the palp reached around the eye, first contacting it posteriorly. The maxillipede then recoiled, working the triserrate setae of the propodus and dactylus (Fig. 10B, D) around the eye, down the eyestalk, and across the interorbital area, usually including the antennae. The cuspidate setae of the carpus were sometimes brushed over the orbit lip and epistome. As Crane (1975) observed for fiddlers, the act moved from distal to proximal – uncommon for a unidirectional grooming act. The palps, at times, scrubbed the interorbital area without grooming the eyestalks. The third maxillipedes, together with the second maxillipedes, also cleaned the tips of the chelipede fingers. After a series of grooming acts, the third maxillipedal palps scrubbed against each other and against the second maxillipedes. Debris was dropped to the substrate, ingested, or picked away by a chelipede. The epipods of the maxillipedes swept the gill surfaces as a direct result of endopodal movements and/or their own musculature, thus dragging the epipodal setae (Fig. 11A, B) across the gills. Such epipodal grooming is a common brachyuran feature (Borradaile 1922, Hiatt 1948, Vuillemin 1967, Walker 1974, Warner 1977, Bauer 1981, this volume).

The dense stands of triserrate setae (Figs. 9D, 10B), with their comb-like serrations, were clearly the dominant grooming setae of the maxillipedal palp, although they also helped support large morsels during feeding (pers. obs.) and could function as chemo- and/or mechanoreceptors, as Derby (1982) found for some serrate setae. The cuspidate setae served in grooming, as well. The role of the pappose setae is somewhat more problematical. Some pappose setae, particularly those of the lateral edges of the proximal propodus and distal carpus, did come in contact with the antennae and interorbital area during grooming, and Farmer (1974) has suggested that pappose setae function in the cleaning of adjacent mouthpart structures. Nevertheless, pappose setae seem rather delicate and fragile in comparison to the typically robust and strongly serrate grooming setae of decapod crustaceans (Roberts 1968, Thomas 1970, Bauer 1975, 1977, 1981, Hindley & Alexander 1978, Schembri 1981, 1982a, b). Alternatively, Thomas (1970) has hypothesized a supporting role in food collection and transfer, and Schembri has proposed a mechanical function, as screens, gaskets, etc. (1981) or a sensory (1982b) role for pappose setae.

The chelipedes were also often used to groom the eyestalks, which was somewhat surprising in view of the disparity of size and strength of the two structures. The chelipede(s) delicately grasped the eyestalk near the base and brushed along its surface. An eyestalk was groomed by the ipsilateral or contralateral chelipede or both chelipedes in unison. A chelipede dactylus also often scrubbed the orbit. The branchiostegite was groomed by three different methods. 1) The concave chelipede merus and ischium circularly scrubbed the convex branchiostegite, and occasionally the lateral carapace, with the stout simple setae of the inner surfaces (Fig. 11C) combing the branchiostegite setae. 2) With fingers somewhat separated, the contralateral chelipede tips (sometimes just the dactylus) brushed the branchiostegite from ventrolateral to dorsomedial. As the fingers neared the buccal area, they were apposed and were cleaned by the maxillipedes. 3) The contralateral chelipede picked at clumps of debris fouling the branchiostegal setae. This picking sometimes extended to the thoracic sterna and abdomen. A chelipede groomed its opposite either by picking at the other's surface with the finger tips or by scrubbing the outer propodus and dactylus against the inner propodus of the other claw. Material gathered from the body was either transferred to the maxillipedes or wiped against the substrate.

Mutual scrubbing of the pereiopods (including the chelipedes) was a rather common occurrence and was accomplished in three ways. 1) The posterior surface of an appendage and the anterior surface of the following leg were scrubbed together. 2) Two pereiopods crossed over each other, with the forward pereiopod's anterior surface thus scrubbing against the posterior of the following appendage. 3) Two appendages (e.g., the second and fourth pereiopods) met over the depressed intervening appendage, with the posterior of the leading leg and the forward edge of the posterior leg performing a mutual scrub. At times, all ten pereiopods were involved in mutual scrubs simultaneously, although the chelipedes did not perform the latter two types of movements. The second pereiopod sometimes used its narrow lateral edge or dactylus tip against the chelipede.

As in *Coenobita clypeatus*, grooming in *Cardisoma guanhumi* was most frequent and intense following rain or when the animal was in standing water. If the water was deep enough, the anterior carapace submerged by tilting forward, and the eyestalks were washed by repeated dips into the water-filled orbits.

Foam bathing, in which bubbles produced by the mouthparts disperse fluid about the body, occurred in partially submerged or emergent crabs. This action has been variously interpreted as a method of thermoregulation (Altevogt 1968), pheromone distribution (Wright 1966), water reserve aeration (Lindberg 1980, Jacoby 1981), or cleansing (Schöne & Schöne 1963, Brownscombe 1965, Lindberg 1980, Jacoby 1981).

Grooming behavior has also been recorded from a number of other amphibious crabs. Pearse (1912), investigating *Uca* (grades 1+ to 3), noted that the walking legs and chelae are grooming appendages and emphasized attention to the eyestalks. Crane (1975) stated that submersion is the major cleansing method in fiddler crabs. She also recorded the grooming of the eyestalks by 1) depression into wet sockets, 2) grasping with the chelae, or 3) brushing by the third maxillipedal palp. The chelae groom each other, and the first through fifth pereiopods engage in mutual scrubs. She found no obvious interspecific differences. The eyestalks of *Ocypode* (grade 3) are groomed by the palps of the third maxillipede and by setae lining the orbits (Koepcke & Koepcke 1953, Vannini 1980). The minor chelipede is cleaned by the maxillipedes and the major by the adjacent two walking legs (Vannini 1980), and the mouthparts scrub each other (Koepcke & Koepcke 1953).

The soldier crab, *Mictyris longicarpus* (Mictyridae) (grade 2), performs what must certainly be the most acrobatic grooming movement recorded from the Brachyura. According to Cameron (1966), the crab, following emergence, falls on its back, thus removing accumulated sand, and then flips upright again. This 'half somersault' is executed in less than a second. *Mictyris* also grooms the eyestalks and mouthparts with the chelae.

Cott (1929), investigating *Sesarma meinerti* (grade 3), described the grooming of the branchiostegal region by serrate setae on the concave surface of the chelipede merus. *Sesarma bidentatum* (3) and *S.verleyi* (3) also use serrate setae on the concave merus to groom the branchiostegite, while *S.reticulatum*, *S.rubinofforum*, *S.rectum*, *S.aequatoriale* (all grade 3), and *S.jarvisi* (4+) use in addition setae on the carpus (Felgenhauer & Abele 1983). The latter authors also recorded the grooming of the epistomal region of *S.reticulatum* by the setae on the third maxillipedal palp. Alexander & Ewer (1969) also emphasized the use of stout meral setae in branchiostegal grooming in *S.catenata* (3) and *Cyclograpsus punctatus* (3). The mouthparts, eyes, and antennae are groomed by setae on the palp of the third maxillipede. The chelae pick at the mouthparts, the branchiostegite, the sterna, and the pereiopods and scrub the eyes, antennae, and mouthparts with tuberculate ridges on the propodi. The walking legs engage in mutual scrubs with the chelae and each other. These grapsids, like fiddler crabs, also clean themselves by submersion. Lindberg (1980) and Jacoby (1981) described action patterns from *Hemigrapsus oregonensis* (2) and *H.nudus* (2), respectively. They report virtually identical behavior: the chelipedes rub or pick at the buccal area, thoracic sterna, abdomen, and opposing chelipede; the legs scrub each other, and the third maxillipedal palp cleans the eyestalk. Jacoby called attention to the close resemblance between aquatic and amphibious brachyuran grooming behavior.

Wright (1966) recorded grooming from a variety of grade 4 (*Gecarcinus quadratus*), grade 3 (*Cardisoma crassum*, *Ucides occidentalis*, *Grapsus grapsus*, *Goniopsis pulchra*), and grade 2 (*Pachygrapsus crassipes*, *P.transversus*, *Sesarma sulcatum*, *Hemigrapsus oregonensis*, *H.nudus*, and *Goetice americanus*) crabs of the families Gecarcinidae and Grapsidae. Like Jacoby (1981), Wright stressed the similarity of grooming in these species, stating that 'all cleaning patterns seen in one species also are seen in the others.' The chelae scrub each other, the mouthparts, the sterna, the abdomen, and the eggs of females in berry. The eyestalks are groomed by the typical movements of the third maxillipedal palps, while the walking legs scrub each other, the chelae, and sometimes the ventral body. Wright emphasized the secondary role of grooming as a displacement activity (intense, incomplete, and nonfunctional behavior evoked by the thwarting of one or more drives) in these species, as did Crane (1957, 1975) for ocypodids.

There does, indeed, seem to be remarkable similarity of grooming behavior noted in the above reports. Grooming of the eyestalks by the third maxillipedal palp is obviously a prevalent movement, as is scrubbing of the branchiostegite by the chelipede merus, grooming of the mouthparts and opposite chelipede by the chelipede fingers, and mutual pereiopod scrubbing. Based on the available information, there is no indication of marked differences in brachyuran grooming behavior as a response to varying degrees of terrestriality.

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