

Grooming behaviour and the morphology of grooming appendages in the endemic South American crab genus *Aegla* (Decapoda, Anomura, Aegliidae)

J. W. MARTIN AND B. E. FELGENHAUER

Department of Biological Science, Florida State University, Tallahassee, Florida 32306 USA

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Grooming behaviour in South American freshwater aeglid crabs (*Aegla platensis* and *A. uruguayana*) involves primarily the third maxillipeds and fifth pereiopods. The third maxilliped grooms the eyes, antennules and occasionally the antennae with fields of sword and serrate setae. The crista dentata located on the ischium of the third maxilliped cleans the dactyli of the second, third and fourth pereiopods. The fifth pereiopod is chelate but opens only slightly. This appendage grooms the gills, carapace, abdomen and pleopods with the denticulate margins of the chela and specialized composite setae of the propodus and dactylus. Grooming behaviour and general morphology of grooming appendages in aeglids resemble those of their marine relatives in the Anomura rather than those of other freshwater decapods. This observation supports Bauer's (1981) contention that grooming may serve as an indicator of phyletic affinity.

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Introduction

Grooming behaviour and the morphology of grooming appendages in decapod Crustacea were reviewed by Bauer (1981). Grooming appears to be widespread throughout the Decapoda, with the primary function being the removal of fouling organisms or particulate matter. The study of grooming behaviour and morphology in decapods is of interest not only in itself, but may play an important role in assessing phylogenetic relationships (Bauer, 1981; Reese, 1983).

Grooming behaviour in some groups, such as the Caridea, is well known (Wickler & Seibt, 1970; Bauer, 1975, 1977, 1978, 1979; Wasserthal & Seibt, 1976; Fryer, 1977; Felgenhauer & Schram, 1978, 1979; Felgenhauer & Abele, 1983), but in other taxa grooming and associated morphology of grooming appendages have received little attention. For the Anomura, examples of grooming are rare (see Discussion). Bauer (1981) observed or inferred (from morphology) grooming in at least one species of axiid, callianassid, galatheid, porcellanid, pagurid, lithodid

TABLE I
Reported epibionts and parasites from Aegla

Epibiont/Parasite	Location on Aeglid	Reference
Filamentous algae	carapace	Bahamonde & Lopez, 1961
Diatoms	carapace	" "
Rotifers	carapace	" "
Bacteria	carapace	Burns, 1972
Protozoa		
<i>Epistylis</i> sp.	carapace, gills	Mouchet, 1931 <i>a, b</i> ; 1932
<i>Lagenophrys aeglea</i>	gills	Mouchet, 1931 <i>a, b</i> ; 1932
Vorticellids	carapace, gills	Bahamonde & Lopez, 1961
Annelida		
<i>Stratiodrillus aeglaphilus</i>	gill chamber	Vila & Bahamonde, 1985
<i>Stratiodrillus platensis</i>	"	Cordero, 1927
" "	"	Mouchet, 1931 <i>a, b</i> ; 1932
" "	"	Harrison, 1928
" "	"	Roubad, 1963
<i>Stratiodrillus</i> sp.	"	Bahamonde & Lopez, 1961
" "	"	Dioni, 1972
Platyhelminthes		
<i>Didymorchis</i> sp.	carapace	Dioni, 1972
<i>Temnocephala chilensis</i>	gills	Dioni, 1967 <i>a, b</i>
" "	"	Porter, 1906
" "	abdomen	Bahamonde & Lopez, 1961
<i>Temnocephala axenos</i>	gills	Dioni, 1967 <i>a, b</i>
<i>Temnocephala bresslaui</i>	carapace	Gonzalez, 1949
<i>Temnocephala mexicana</i>	carapace	Dioni, 1972
<i>Temnocephala</i> sp.	ubiquitous	Mouchet, 1931, 1932
Crustacea		
Lernaeid copepod	gills	Bahamonde & Lopez, 1961

and hippid; several of these examples were taken from previous accounts in the literature (see Bauer, 1981, table I).

The endemic South American crustacean family Aegliidae consists of a single genus *Aegla* known from lakes, streams, swamps and caves from most of temperate South America (Hobbs, 1979). Aeglids are the only members of the Anomura entirely restricted to freshwater. Although it is a large group, our knowledge of the family is wanting. Aeglids are known to harbour a large number of epibionts, including bacteria, diatoms, peritrichous ciliates, flatworms, rotifers, annelid worms and copepods (Harrison, 1928; Bahamonde & Lopez, 1961; Dioni, 1967*a, b*; Burns, 1972) (see Table I). However, grooming behaviour in aeglids has not been previously reported. Because aeglids are the only freshwater members of the predominantly marine Anomura, yet are similar in many ways to freshwater astacoid crayfish in their life history, they represent an excellent opportunity to explore grooming behaviour and morphology as a convergent adaptation to habitat versus its value as an indicator of phyletic affinity.

Materials and methods

Aeglid crabs (*Aegla platensis* Schmitt, 1942 and *A. uruguayana* Schmitt, 1942) were collected in April, 1984, from the Arroyo San Antonio in southern Uruguay and transported in styrofoam chests to aquaria in Tallahassee, Florida. Artificial habitats were constructed by placing rock rubble and bricks into 7.5 litre

aquaria. Approximately 50 aeglids were placed in each of 4 aquaria. Aeglids were observed at irregular intervals. Both diurnal and nocturnal behaviour were monitored. No attempt was made to determine differential grooming effects of individual appendages by amputation, and no artificial or additional fouling matter was added to the aquaria.

Illustrations are from observations and photographs of laboratory animals. Specimens used for scanning electron microscopy (SEM) were fixed in 10% formalin or 3% glutaraldehyde in 0.1 M phosphate buffer for 3 h and postfixed in 2% osmium tetroxide for 1.5 h at room temperature. Fixed tissue was cleaned by sonication, dehydrated in a graded ethanol series and critical-point dried. Specimens were then mounted on stubs and sputter coated with 20 nm of gold palladium for observation in a Cambridge S4-10 scanning electron microscope at accelerating voltages of 5–30 kV.

Results

Epibionts

Epibionts known to occur on aeglids are listed in Table I. Our specimens did not harbour all of the reported epibionts. We encountered a large number of protozoans, notably *Epistylis*, on the antennae, antennules, mouthparts, carapace and thoracic appendages. A second protozoan, *Lagenophrys*, was abundant on the gill surface of certain individuals, especially so between the posterior (proximal) gill lamellae. The flatworm *Temnocephala* was found on the carapace of a single individual. The most easily observed fouling organisms were the numerous egg cases of aquatic worms. These cases remain on the aeglid cuticle long after the developing worm has left the case. Eggs of aquatic trematodes were also encountered on the distal foliose portion of the gills. Filamentous algae were found on the carapace of most individuals.

Grooming behaviour

Eyes

The distal segment of the third maxilliped is rarely passed over the dorsal surface of the eyestalk. To facilitate this cleaning, the eyestalk is briefly deflected ventrally.

Antennules

Flicking motion by the antennules is continuous. Grooming is accomplished by deflecting the antennule ventrally toward the third maxilliped. The dorsal and ventral branches of the antennule are then drawn through the area between the densely setose propodus-dactylus and merus-carpus portions of the third maxilliped (Fig. 1a). During this time, the second maxillipeds are also actively deflected laterally and dorsally, but their value in grooming the antennules is difficult to ascertain.

Antennae

Antennal cleaning is via the third maxillipeds. The antennae are passed between the distal portions of the third maxilliped and drawn back against the setae of the dactylus, propodus and carpus. The antennae are occasionally drawn through the opening of the cheliped, but it is not clear if this is intentional or accidental. The length of the antennae, coupled with the fact that the chelipeds are not closed during these instances, leads us to suspect that this action is incidental and does not constitute grooming as defined by Bauer (1981).

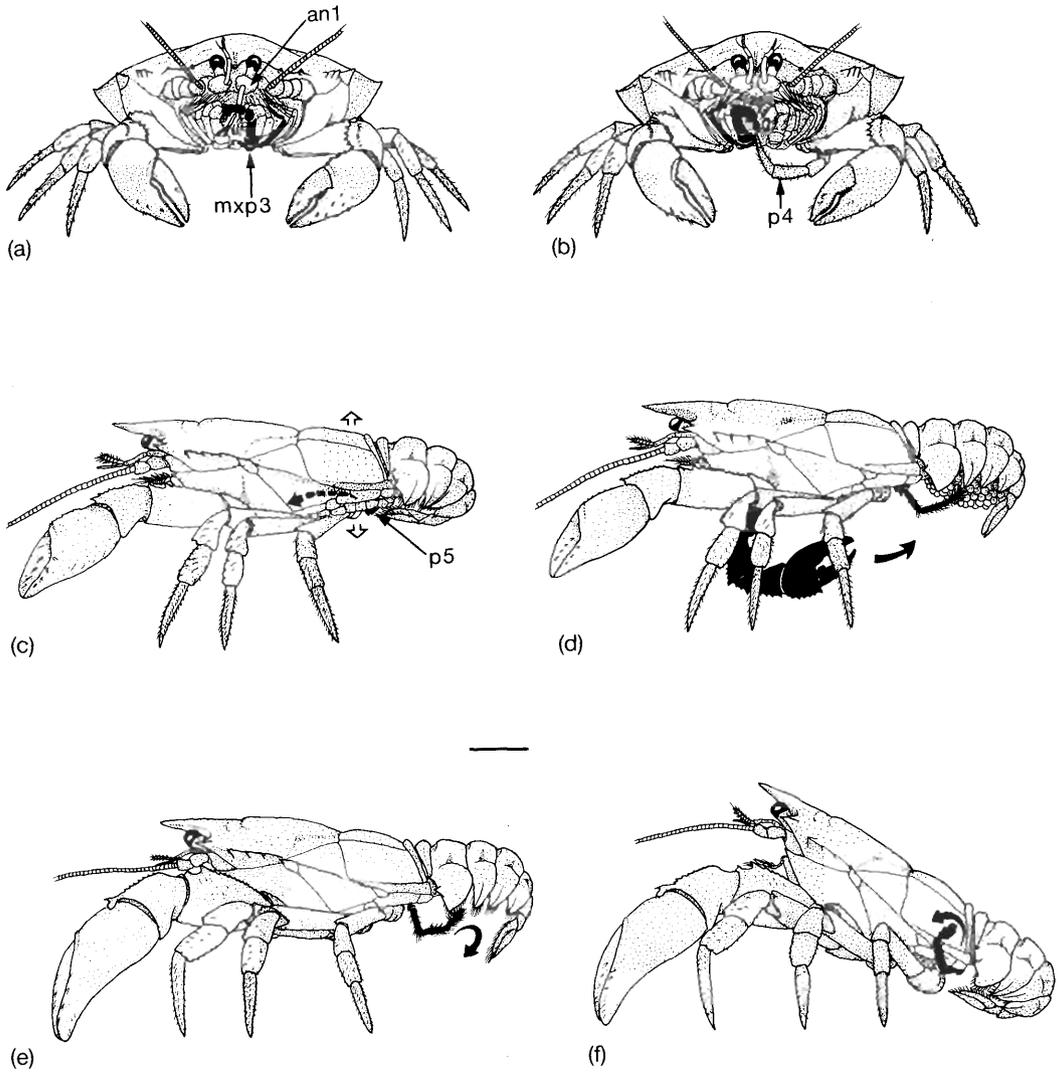


FIG. 1. Grooming behaviour in the freshwater crab genus *Aegla*. (a) Grooming of the left antennule (an1) with the left third maxilliped (mxp3, in black). (b) Grooming of the dactylus of the left fourth pereiopod (p4) with the crista dentata of the right third maxilliped (in black). (c) Lateral view of aeglid showing approximate reach of fifth pereiopod (p5, in black) within branchial cavity; black dashed arrow denotes p5 movement within branchial chamber; white arrows denote expanded carapace facilitating this behaviour. (d) Ovigerous female cleaning egg mass with p5 and right cheliped (in black); arrow denotes movement of abdomen and cheliped towards each other for grooming. (e) Male cleaning abdomen with p5 (in black) removed from beneath carapace; arrow denotes movement of p5. (f) Male in resting position cleaning posterior carapace with p5 (in black). Scale bar = 1.0 cm.

Branchiae

The gill chamber is commonly fouled by a variety of organisms. The gills harbour, between lamellar sheets on the posterior (proximal) half of the gill, a large number of stalked protozoans. Gills are flushed regularly by the pumping action of the scaphognathite. Water enters the branchial chamber through openings at the base of the cheliped and posterior thoracopods and exits through the oral region. The current can at times be reversed, possibly functioning to some extent as an antifouling adaptation. The fifth pereopod normally rests within the branchial chamber and is withdrawn only briefly for grooming other areas (see below). The minutely chelate fifth pereopod and its accompanying setal brush function in grooming the posterior gills (Fig. 1c). The fifth pereopod is bent sharply at the basi-ischial joint to accommodate insertion into, and cleaning of, the branchial chamber. To facilitate this grooming, the carapace is inflated dorsoventrally by expansion of the posteroventral plates. There is no epipod-setobranch system on any of the pereopods.

Pereopods

The second, third and fourth pereopods terminate in a narrow dactylus with an acute, corneous, recurved tip. Rows of setal groups occur in pits along the anterior and posterior surfaces of the dactylus. These dactyli are occasionally groomed by insertion into the mouth region between the third maxillipeds (Fig. 1b). It appears that, in addition to the serrate setae of the distal segments, the crista dentata of the fused basi-ischium functions in scraping the surfaces of the inserted dactylus.

Pleopods

The pleopods of the female are routinely groomed by the chelate fifth pereopod. To facilitate this grooming, the female raises herself by straightening her pereopods until no part of the thorax or abdomen is in contact with the substratum. The fifth pereopods are then removed from their normal position within the branchial chamber and passed along the ventral surfaces of the abdominal somites, over the pleopods (Fig. 1e). The fifth pereopods do not function synchronously but rather appear to work independently. This behaviour increases prior to egg deposition. Males lack pleopods and perform this behaviour less often, probably for grooming of the abdominal sterna.

Eggs

Ovigerous females carry eggs on the well-developed pleopods. The egg mass is groomed often by the fifth pereopods. The behaviour is similar to that described above for pleopod grooming. Occasionally, the first pereopod (cheliped) is inserted between the flexed abdomen and the thorax (Fig. 1d), probably for grooming (removal of debris).

Abdomen

Males and non-ovigerous females groom the ventral surface of the abdominal somites as described above for pleopod grooming (Fig. 1e). In addition, the fifth pereopod sometimes passes over the external ventral half of the pleura of the abdominal somites when the abdomen is flexed.

Carapace

The fifth pereopods can reach only the posterolateral and posterodorsal areas of the carapace

(Fig. 1f). This behaviour is rare and of questionable significance, as the portions of the carapace reached by that appendage do not appear to be any less fouled than other areas of the carapace.

Autogrooming

When not actively grooming other appendages or body regions, or involved with feeding, the third maxillipeds autogroom (self clean) by brushing against each other briskly in a ventral plane. The mesial elevated fields of serrate and sword setae on the propodus and carpus are rubbed against those on the opposing appendage.

Morphology of grooming appendages

Third maxilliped

The third maxilliped is pediform and well developed. A variety of setal types occurs on many of the segments (Fig. 2a). Grooming is likely confined to the carpus, propodus and dactylus. The carpus and propodus bear medial ovate fields of serrate, stout serrate, comb and sword setae (Fig. 2a, Plate I(c-e)). These fields are slightly elevated with respect to the surrounding cuticle. The dactylus (Plate Ia) bears numerous setal types, most obvious of which are the stout serrate setae (Plate Ib) and comb setae. The crista dentata of the ischium is directed mesially. It consists of a row of large corneous teeth, with the distal-most tooth the largest (Fig. 2a, Plate If). The primary function of the crista dentata is probably maceration of food, but it may also function in scraping the dactyli of the pereopods. Whether the primary objective of inserting the pereopod dactylus into the oral region is to groom that segment or to bring food particles into the mouth is not known. The epipod (ep, Fig. 2a), an important gill-cleaning structure in many decapods (see Bauer, 1981), is reduced and non-functional in aeglids and lacks setobranch setae.

Fifth pereopod

The fifth pereopod is of primary importance in grooming. Although the appendage is truly chelate (Fig. 2b, Plate I(c)), the claw is small and cannot open widely. Manipulation of the chela in preserved specimens almost always resulted in damage to the appendage. The chela consists of a reduced dactylus and an elongate cylindrical propodus that meet in a sinuous border (Plate IIa, b). The borders of the chela bear curved sclerotized teeth, those of the dactylus overlapping those of the propodus (Plate I(c)). These teeth bear a double row of stout serrations on the internal margin (not visible in Plate I(c)). In addition, the propodus bears a second row of stout short scale setae behind (proximal to) the teeth of the chela (Plate I(c), arrows; Plate I(d)).

The propodus and dactylus bear numerous long setae proximal to the chela borders (see Plate IIa) which, under light microscopy, appear simple. Under high magnification, many of these setae appear to be composite setae, with a distally directed double row of sharp setules and a proximally directed border of minute papillae (Plate IIe, f). The density of these setae, their absence on other appendages, and the limited functional ability of the chela suggest that the propodus and dactylus function as a grooming brush for the gills. This brush is likely to be of more importance in grooming than is the reduced chela of the same appendage. Long simple setae are interspersed among the composite setae.

Discussion

The genus *Aegla* is unique in many respects among the decapod Crustacea. Morphologically, aeglids differ from other members of their assigned superfamily (Galatheoidea) in a number of

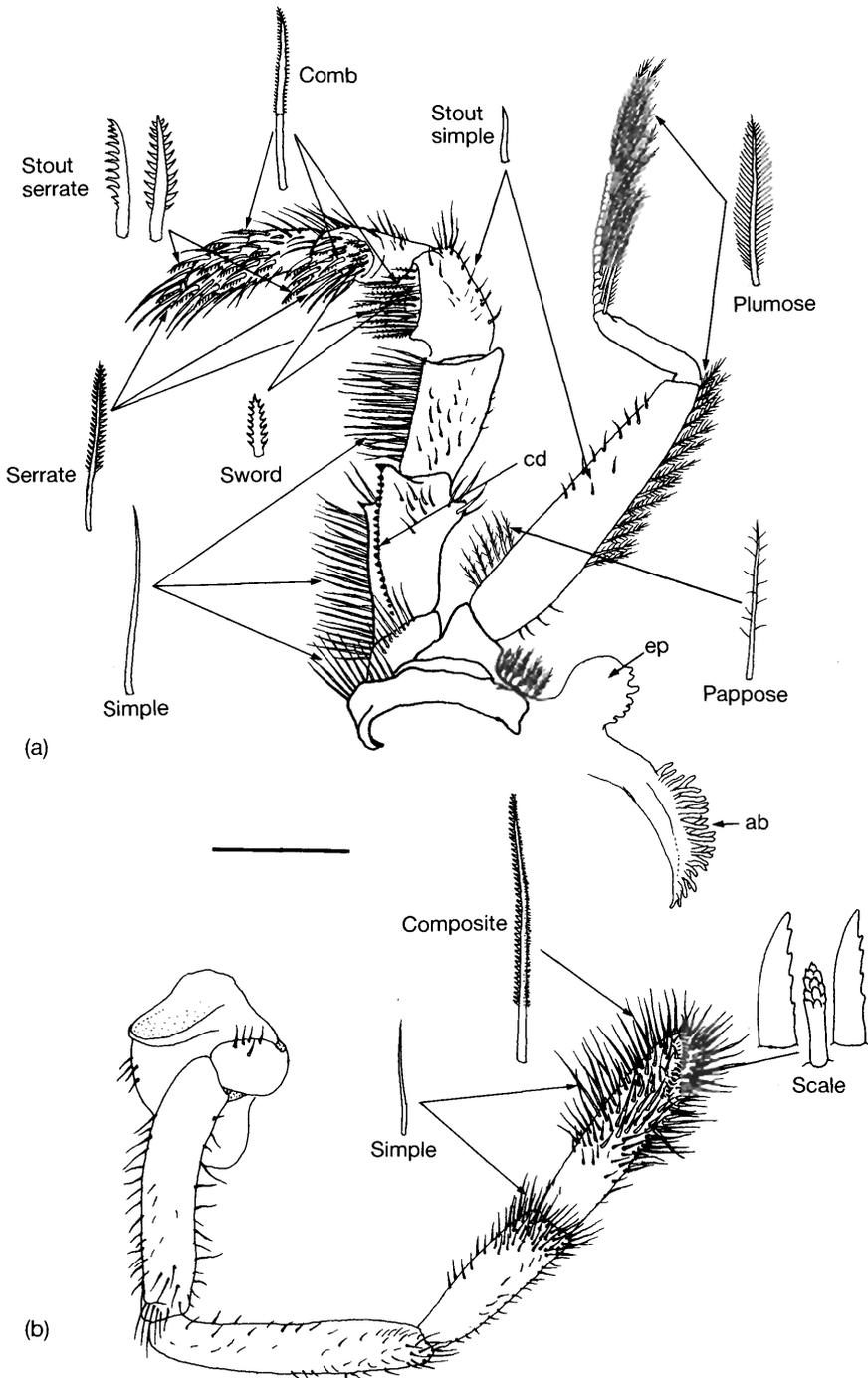


FIG. 2. Setal types and approximate location on grooming appendages: (a) third maxilliped; (b) fifth pereiopod. Arrows indicate areas of high likelihood of encounter for a given setal type and are not inclusive or exclusive of occurrence. cd = crista dentata; ep = epipod; ab = arthrobranch gill. Scale bar = 2.0 mm.

characters. Examples are the dimorphic first chelipeds, reduced gill number, and presence of dorsal carapace sutures. Ecologically, they are similar in some ways to freshwater reptant decapods in other families (e.g. astacoid and parastacoid crayfish, pseudothelphusid and trichodactylid crabs), but in other ways have no parallel among the Decapoda. For example, aeglids are reported to leave the water and congregate beneath stones or logs at the water's edge during the spawning period, when they may be found in association with spiders, scorpions and isopod crustaceans (Bahamonde & Lopez, 1961; Burns, 1972). Their grooming needs and/or mechanisms therefore might be expected to differ greatly from those of marine anomurans or freshwater decapods in other infraorders.

Because the ultimate goal of grooming is the removal of fouling material, it is not surprising to see striking convergences among setal types modified for this purpose. Aeglid setal types are essentially identical to those described for the mouthparts of hermit crabs by Kunze & Anderson (1979), with few exceptions. The distinctive sword setae of *Aegla* (Plate Ic, d) are not known for hermit crabs, although further examination using electron microscopy may reveal in hermits setal types as yet undetected (e.g. see Schembri, 1982). The composite setae of the fifth pereiopod (Plate IIe, f) appear unique to *Aegla* as well. Although we know of no other similar seta among the Decapoda, a setal type bearing teeth along one border and spines along the other is known in stomatopod crustaceans (Jacques, 1981, fig. 11). These setae probably do not differ in function from the simpler comb and serrate setae of other decapod grooming appendages.

Grooming behaviour in marine anomurans has been described for relatively few species. Snow (1973) described antennular grooming in the hermit crab *Pagurus alaskensis* (Benedict) and noted the importance of grooming in prevention of antennular fouling in hermit crabs. Schembri (1982) described autogrooming of the mouthparts and grooming of the anterior carapace and appendages in the hermit *Pagurus rubricatus* (Henderson). Gonor & Gonor (1973) mention grooming in postlarval stages of four species of porcellanid crabs. Grooming in adult porcellanids was described by Nicol (1932) and by Ritchie & Hoeg (1981) as an adaptation to avoid infestation by rhizocephalan barnacles. Efford (1966, 1971) described antennule cleaning in *Emerita*. MacGinitie (1934) mentions grooming in *Callianassa californiensis* Dana. Bauer (1981) observed or deduced grooming in axiids, callianassids, galatheids, porcellanids, pagurids, lithodids and hippids. In nearly all cases, the main grooming appendages are the third maxilliped and the fifth pereiopod, which typically bear numerous types of serrate, comb or spinose setae to facilitate grooming. Thus, grooming behaviour for marine anomurans parallels that for the freshwater Aegliidae. Gill cleaning in all groups (aeglids and marine anomurans) is by the chelate fifth pereiopods, with the exception of axiids which possess epipodal setobranch setae (see Bauer, 1981 for definitions) for that purpose. General body grooming for all groups is via pereiopods 4 and 5 (axiids and callianassids) or pereiopod 5 (*Anomura sensu stricto*). In all groups except the hippids (see Efford, 1971), antennule cleaning is accomplished by the third maxillipeds. In aeglids as well as in most other anomurans, the antennules are the most often groomed appendage, probably because of their valuable role as sensory organs in the Decapoda (Snow, 1973; Bauer, 1975, 1977).

In contrast to marine anomurans, in the freshwater cambarids *Procambarus clarki* and *Austropotamobius pallipes* the antennules are groomed by the third maxillipeds, but the gills are groomed by coxal setobranch setae (Bauer, 1981; Thomas, 1970). This method of gill cleaning (setobranch setae) is similar to that seen in 'primitive' marine reptants (see Bauer, 1981). Reports of grooming in other freshwater reptants are unknown. We have examined preserved specimens of freshwater crabs of two families (Pseudothelphusidae and Trichodactylidae). In both families, the epipod

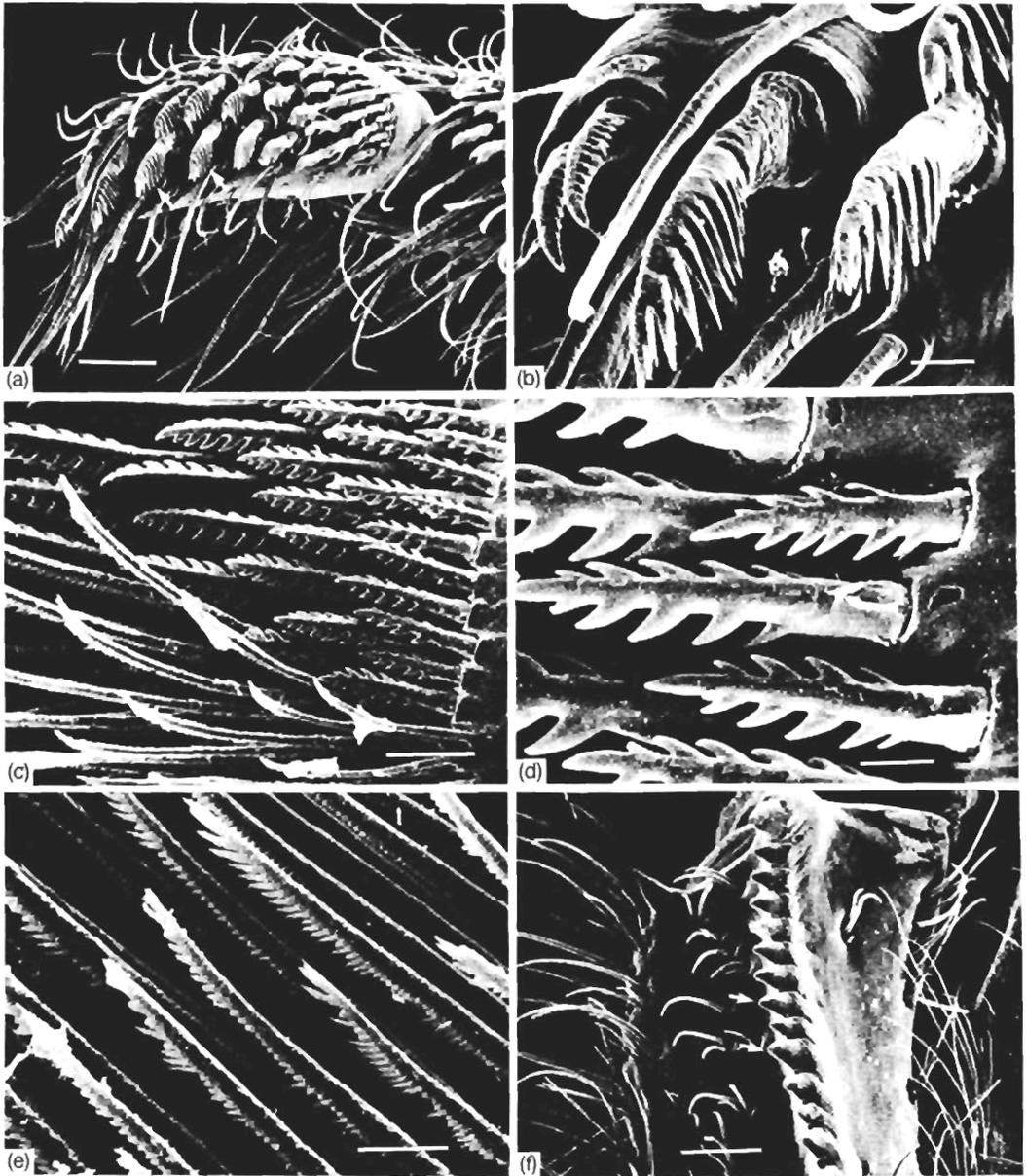


PLATE I. Grooming morphology of the third maxilliped. (a) Dactylus, mesial view with numerous stout serrate setae. Scale bar = 200 μm . (b) Stout serrate setae of dactylus magnified from (a). Scale bar = 50 μm . (c) Field of sword setae on propodus, mesial view. Scale bar = 50 μm . (d) Sword setae of propodus, higher magnification. Scale bar = 20 μm . (e) Serrate setae of propodus. Scale bar = 20 μm . (f) Crista dentata of ischium of third maxilliped, mesial view. Scale bar = 250 μm .

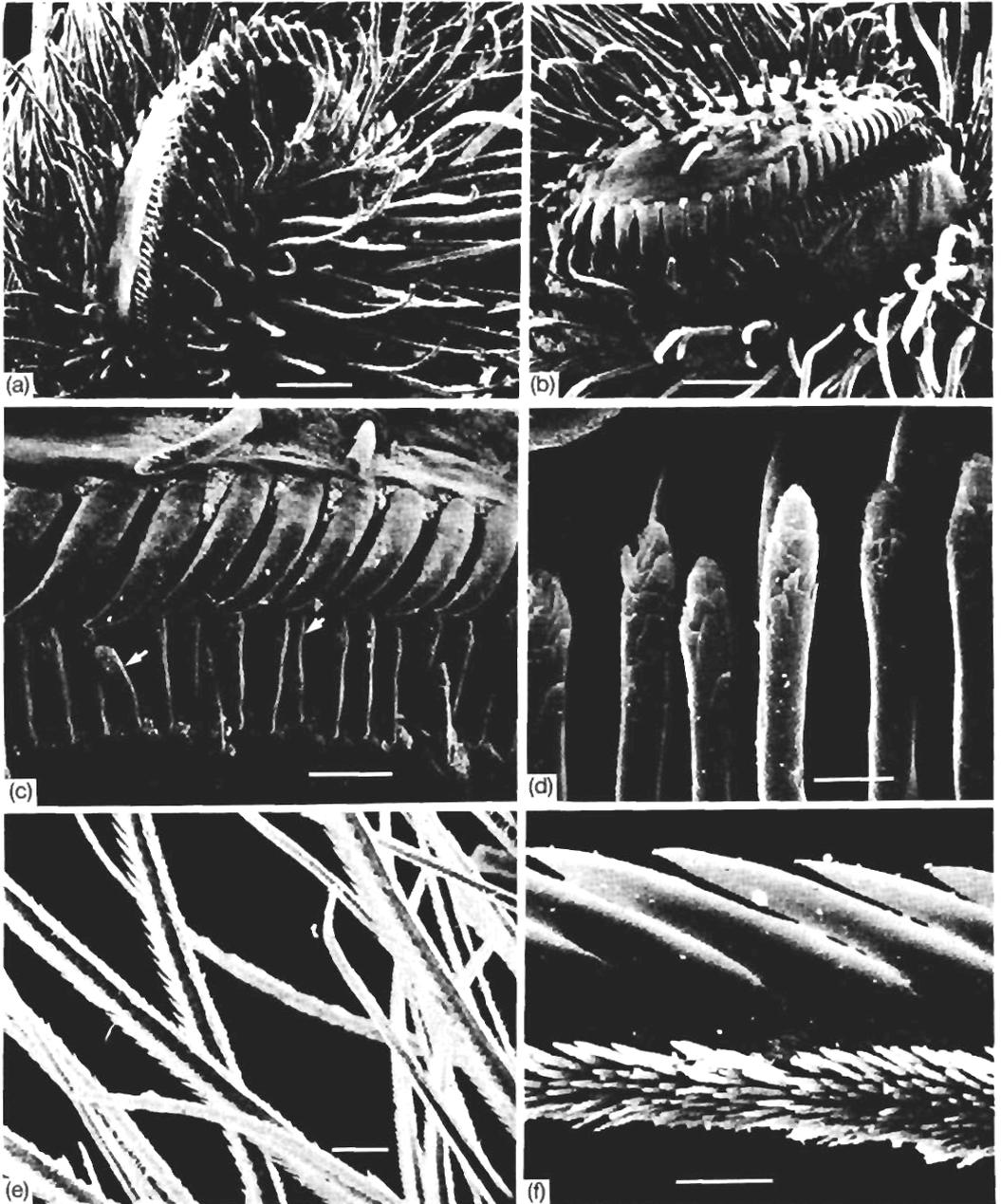


PLATE II. Grooming morphology of the fifth pereiopod. (a) Chela formed by dactylus (on left) and propodus, lateral view. Scale bar = 400 μm . (b) Same, terminal view, dactylus uppermost. Scale bar = 500 μm . (c) Sclerotized teeth and scale setae (arrows) of chela. Scale bar = 100 μm . (d) Scale setae of dactylus. Scale bar = 20 μm . (e) Long composite grooming setae of propodus. Scale bar = 50 μm . (f) High magnification of grooming seta showing composite nature. Scale bar = 5 μm .

of the first through to the third maxillipeds is elongate and setose and probably functions as a gill-grooming device. This method of grooming is found in all marine brachyurans examined to date (Bauer, 1981). Thus, it appears that grooming behaviour and morphology reflect taxonomic relationship rather than adaptation to habitat. Despite apparently different grooming needs, freshwater decapods employ the same appendages and in the same manner as do their marine relatives. The absence of setobranch setae or setose maxillipedal epipods in aeglids, the only exclusively freshwater anomurans, supports the belief of Bauer (1981) that grooming may serve as a conservative systematic character. That is, they have not adapted the freshwater astacoid or brachyuran mode of gill cleaning, but rather maintain the grooming behaviour and morphology of their supposed marine ancestors among the Anomura.

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