

Morphology of grooming limbs in species of *Petrolisthes* and *Pachycheles* (Crustacea: Decapoda: Anomura: Porcellanidae): a scanning electron microscopy study

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Abstract. The morphology of the grooming limbs, the 5th pair of pereopods, was studied by scanning electron microscopy in six species of porcellanid crabs, *Petrolisthes cabrilloi*, *P. cinctipes*, *P. armatus*, *P. galathinus*, *Pachycheles monilifer*, and *Pachycheles rudis*, and their function was inferred by comparison with findings from previous studies. Grooming limb morphology was almost identical among the four *Petrolisthes* species and differed little compared to that of the two *Pachycheles* species. The 5th pereopods bore a basal tuft of mechanoreceptive setae, three different types of grooming setae armed with setules or denticles, two types of smooth sensilla for location and identification of fouling objects, and a terminal, toothed chela for picking firmly attached objects off the gills and body. The grooming limb was extremely flexible and could reach most parts of the body, including the gill chamber on the opposite side. The grooming limb morphology in *Petrolisthes cabrilloi* is consistent with its well-known effectiveness in preventing parasitism by the rhizocephalan *Lernaeodiscus porcellanae*. Grooming setae remove recently attached cyprids, while the chela can grip and remove the much smaller, firmly attached kentrogons. Porcellanid crabs not known to host rhizocephalans, however, had grooming limbs almost identical to those of *Petrolisthes cabrilloi* despite their previously demonstrated failure to prevent settlement and infestation by *L. porcellanae* larvae. The effectiveness of *P. cabrilloi* in removing kentrogons, therefore, seems also to depend on behavioral adaptations whereby this species recognizes the parasite larvae as high-threat objects.

since fouling of the gills may seriously reduce gas and ion exchange. In the Anomura, the chelate 5th pair of pereopods is reduced and never used walking, and it seems that most if not all anomurans have specialized this pair of appendages as grooming limbs. This may constitute one of the few definite synapomorphies for all Anomura, but the comparative morphology of their 5th pereopods has, nevertheless, received little attention. Bauer (1989) provided a few SEM micrographs from a porcellanid crab, but the only detailed account is by Pohle (1989), who studied both the morphology and function of grooming limbs in the Lithodidae.

For the porcellanid crab *Petrolisthes cabrilloi*, Ritchie and Høeg (1981) investigated the role of pereopodal grooming in defending against infestation by the rhizocephalan *Lernaeodiscus porcellanae*. In the field this porcellanid apparently is almost constantly exposed to female cyprids, which settle on the gills. Parasitization by *L. porcellanae* will not kill the crab but will sterilize it for life. Healthy specimens of *P. cabrilloi* are usually able to remove all parasite larvae from the gills before they succeed in infesting the crab. Interestingly, however, other very closely related species of porcellanids lack this capability (Ritchie and Høeg 1981).

The purpose of this study, therefore, was to examine the morphology of grooming limbs in seven porcellanid species and investigate whether the success exhibited by *Petrolisthes cabrilloi* in circumventing rhizocephalan infestation is due to structural adaptation of the 5th pereopods.

Introduction

Most decapods have one or several appendages specialized for grooming the body (Bauer 1981, 1989). Grooming of the branchial chamber is especially important,

Materials and methods

Porcellanid crabs were obtained from the Pacific coast of USA and Mexico. *Petrolisthes cabrilloi* Glasell was collected at La Jolla, California, from a population infested with the rhizocephalan *Lernaeodiscus porcellanae*, and fixed in 4% formalin in seawater. *Petrolisthes cinctipes* (Randall) was collected at Friday Harbor, Washington, and fixed in formalin. *Petrolisthes armatus* (Gibbes), *Petrolisthes galathinus* (Bosc), *Pachycheles monilifer* (Dana) and *Pachycheles rudis* Stimpson were obtained from the collections of

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the Zoological Museum, University of Copenhagen (now in ethanol; see Haigh 1962).

Whole crabs and ablated grooming limbs were studied and drawn with the aid of a dissection microscope.

For scanning electron microscopy (SEM), the distal part of the grooming limbs was removed by a transverse cut through the carpus and treated as follows: (1) two changes of deionized water; (2) rinse in a very weak solution of dishwasher detergent in deionized water; (3) 8 s treatment in an ultrasonicator while immersed in deionized water; (4) postosmification in 1% OsO₄ buffered with 0.1 M sodiumcacodylate for 20 to 40 min and a rinse in deionized water; (5) dehydration through a graded series of acetone; (6) critical point drying using liquid CO₂. The specimens were mounted on aluminium stubs with nail varnish and studied through a JEOL JSM 840 scanning electron microscope.

The position of gills in the branchial chamber was investigated by removing limbs and carapace from one side of the body and subsequently processing the crab for SEM.

Results

General morphology of 5th pereopods in *Petrolisthes cabrilloi* (Figs. 1 and 2)

In *Petrolisthes cabrilloi*, the 5th pereopods are inserted approximately at the posterior edge of the carapace (Fig. 1). Their general shape is shown in Fig. 2, which illustrates the limbs in their near resting position.

The coxa is a rounded, trough-shaped article with an anterior projection. The very short basis is more or less immovably connected to the ischium, so that these two segments form a functional unit, whose length almost equals that of the propodus. The merus and carpus are slender articles of about equal length, and each is about three times as long as the ischium. The pereopod terminates in a toothed chela, whose movable dactylus is about one third the length of the propodus.

In the resting position, the 5th pereopods, or grooming limbs, are kept wholly outside the gill chamber and folded into a zigzag shape. The ischium and merus extend anterolaterally along the posterior carapace margin and

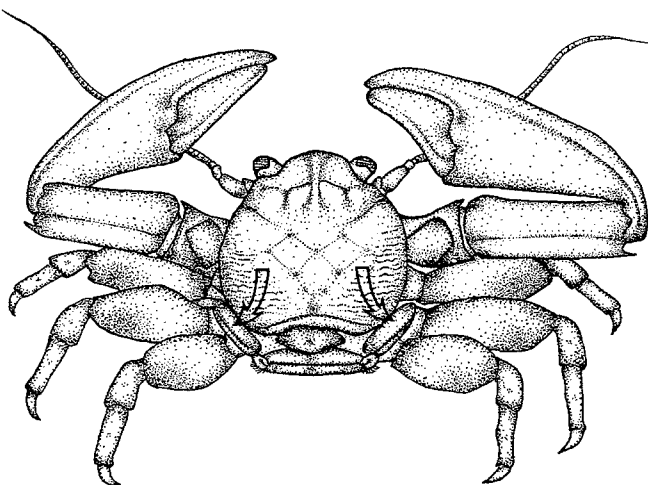


Fig. 1. *Petrolisthes cabrilloi*. Arrows indicate grooming limbs (5th pereopods) in resting position

above the proximal articles of the 3rd and 4th pereopods, whereas an almost 180° bend in the merus-carpus joint allows the more distal articles to extend back towards the limb base.

Most limb joints have extensive areas of arthrodial membrane, which provides the entire appendage with unusual freedom of movement. The 5th pereopods can therefore assume a variety of shapes and their tips can reach most if not all parts of the exterior body surface.

During gill grooming the posterior edge of the carapace is raised and the limb is inserted into the branchial chamber. When fully extended, the grooming limb has about the same length as the carapace, enabling it to reach all parts of the branchial cavity.

Grooming limb setation

The terminology below follows that of Watling (1989). Six distinct types of setae were identified on the 5th pereopods of *Petrolisthes cabrilloi*. Most setae are clustered in groups consisting of one of these six types. Their distribution is indicated in Fig. 2.

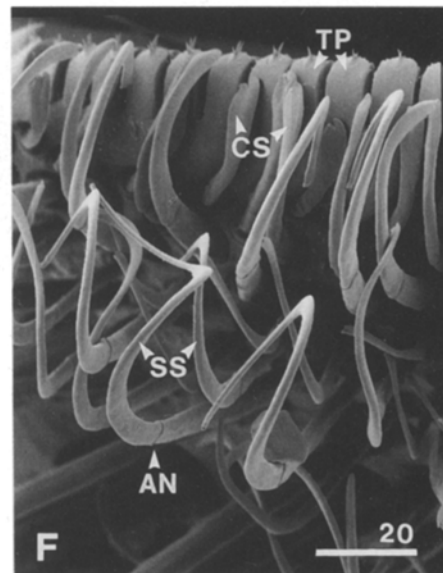
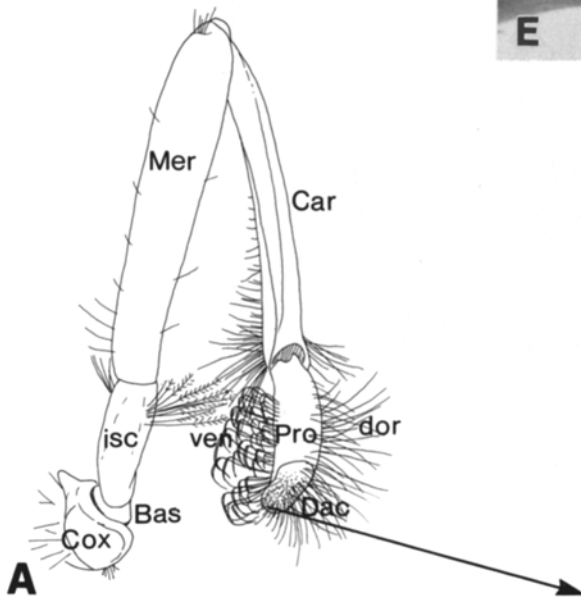
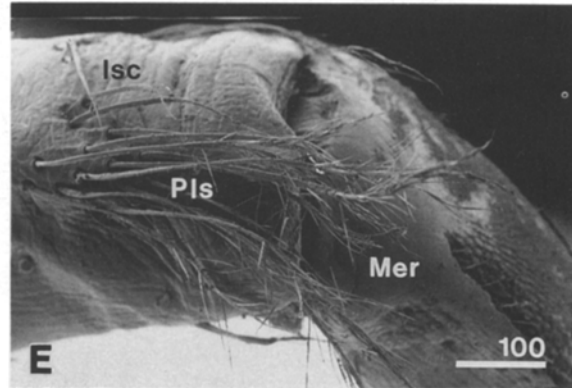
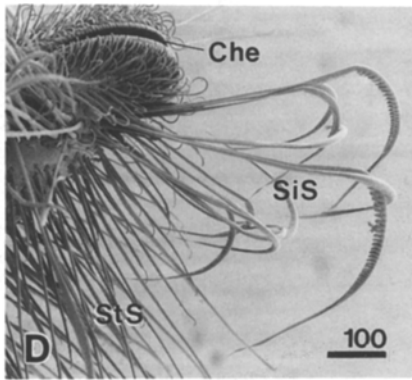
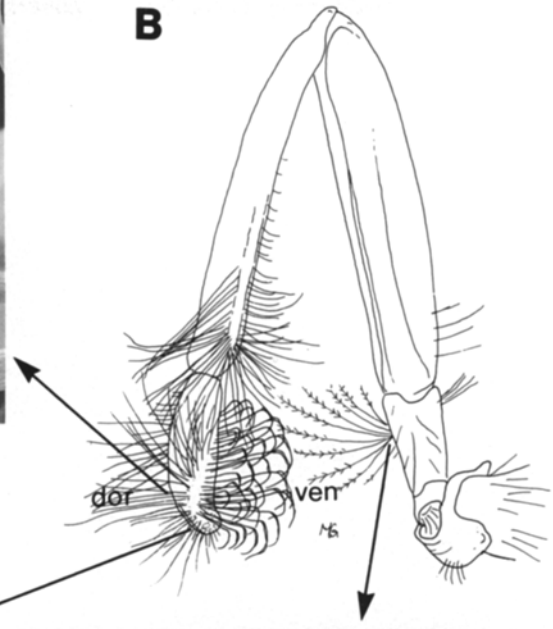
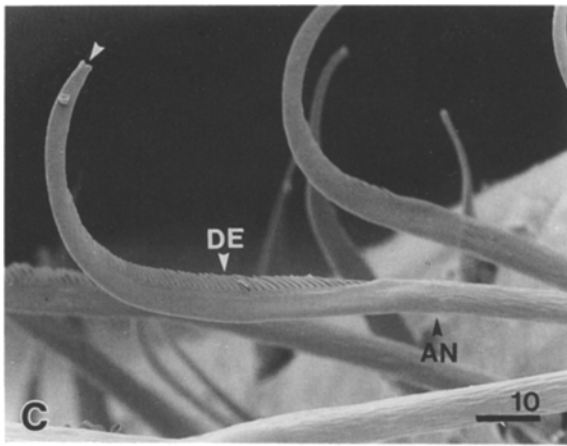
A tuft of plumose setae (Pls, Fig. 2E) extends laterally on the ischium near the joint to the merus. Most remaining limb setae are concentrated on the most distal part of the carpus, propodus and dactylus. All setae on the carpus, propodus, and dactylus have infracuticular articulations and feature an annulus in the form of a cuticular groove encircling the setal shaft.

Type 1. Straight serrate setae (StS, Figs. 2 and 3A to D).

Distribution: In large numbers on the ventral and dorsal sides of the propodus and on the dorsal side of the dactylus. In addition, the carpus bears a group of straight serrate setae ventrodistally, which extend in a fan-like pattern towards the propodus. **Dimensions:** Length < 600 µm; base diameter ca. 10 µm. **General morphology:** Fig. 3D reveals the rather narrow internal lumen. Towards the tip the seta becomes thinner and twisted. A terminal pore was not seen.

The preannular part of the shaft is faintly wrinkled. Postannularly, the seta is adorned with two double rows of closely spaced, slender outgrowths, which point distally along the shaft (Fig. 3C, D). The ventral double row consist of denticles enclosing a median furrow. The out-

Fig. 2. *Petrolisthes* spp. Morphology of the grooming limb (5th pereopod) (A) Dorsal view of right 5th pereopod in near resting position. Grooming setae concentrated on the most distal articles. (B) Ventral view of right 5th pereopod. (C) *P. cincitipes*. Peripheral setae on dactylus. Unlabeled arrowhead designates the bifid tip. (D) *P. cabrilloi*. Terminal chela formed by propodus and movable dactylus, showing groups of sickle setae (SiS) and straight serrate setae (StS) extending ventrally from propodus. (E) *P. cabrilloi*. Tuft of plumose setae (Pls) on the ischium. (F) *P. cincitipes*. Outer margin of terminal chela fringed by club-shaped setae (CS) and smooth setae (SS) with distinct annuli (AN). Other abbreviations: Bas, basis; Car, carpus; Che, chela; Cox, coxa; Dac, dactylus; DE, denticles; dor, dorsal side; isc, ischium; Mer, merus; Pro, propodus; TP, tooth process on chela margin; ven, ventral side. Scale bars in µm



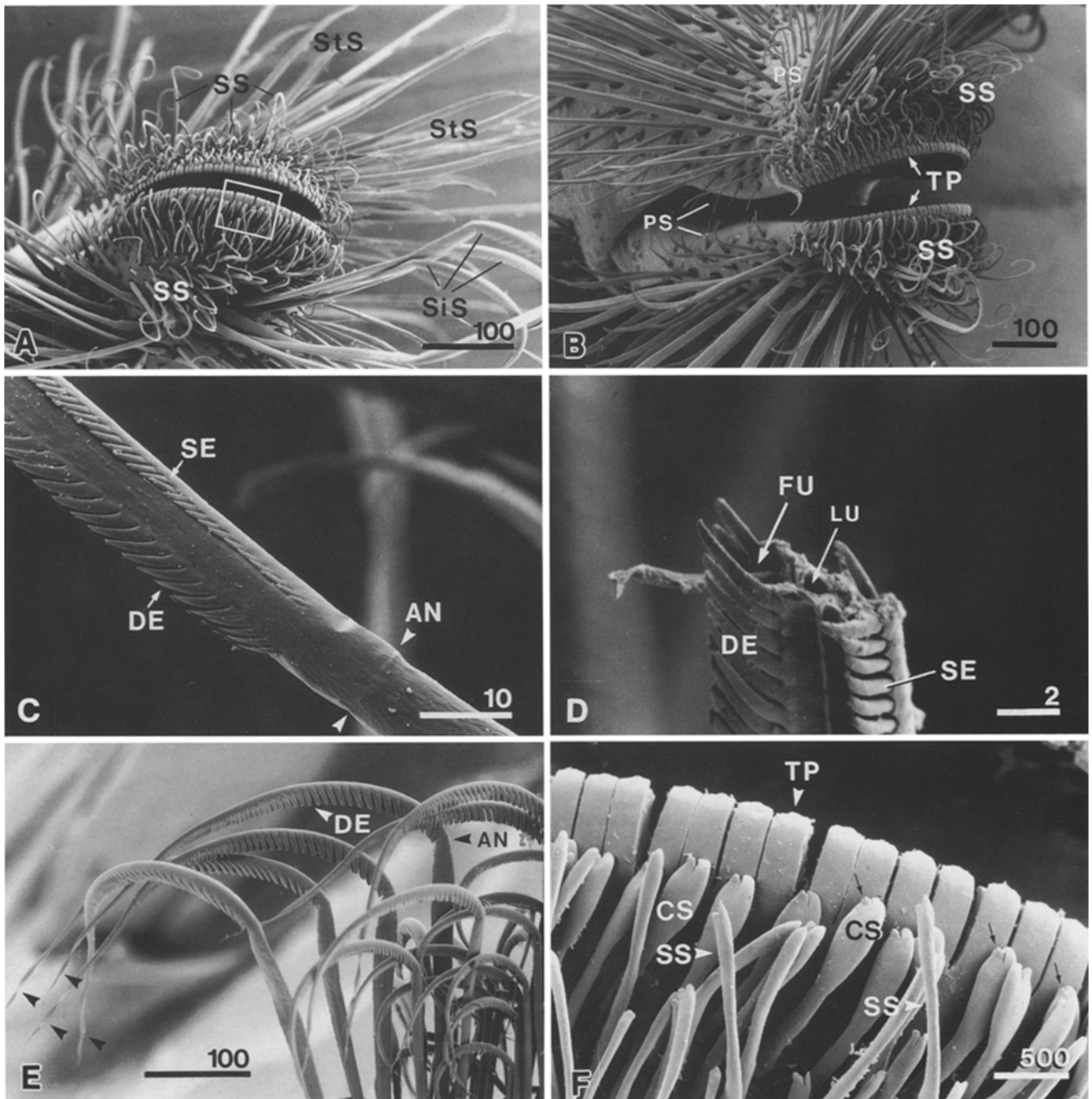


Fig. 3. *Petrolisthes* spp., 5th pereiopod. (A) *P. cabrilloi*. Distal view showing distribution of setae around terminal chela. (B) *P. cinctipes*. Lateral view of terminal chela, showing peripheral setae (PS) in furrow between the two dorsal groups of straight serrate setae on propodus and laterally on propodus and dactylus. (C) *P. cabrilloi*. Straight serrate seta. Proximal part below annulus (AN) displays faint surface wrinkles. (D) *P. cabrilloi*. Broken end of straight serrate seta showing narrow central lumen (LU) and double rows of

denticles (DE) and setules (SE). Note furrow (FU) between rows of denticles. (E) *P. cabrilloi*. Sickie shaped setae with annulus (AN) proximal to denticulated part; terminal shaft part is twisted (arrowheads) and lacks denticles. (F) *P. cabrilloi*. Area within rectangle in (A). Tooth processes (TP) arm the chela margin. Club shaped setae (CS) and smooth setae (SS) exhibit bifid tips. Pores on club shaped setae indicated by arrows. Other abbreviations: SiS, sickie seta; StS, straight serrate seta. Scale bars in μm

growths in the dorsal double row are articulated to the shaft and hence true setules.

Type 2. Sickie-shaped setae (SiS, Figs. 2 D and 3 E). **Distribution:** In two groups on the ventral side of the propodus, one larger and more proximal, the other

smaller and distally located, and whose setae extend obliquely forward, curving around the tip of the chela (Figs. 2 and 3 A). **Dimensions:** Total length 900 to 1000 μm . Length of distal, serrate part of the shaft ca. 400 μm . Base diameter ca. 10 μm . **Morphology:** An almost 90° bend separates the smooth, straight proximal

shaft from the distal curved part, which carries a double row of closely spaced, slender denticles enclosing a distinct furrow (Fig. 3E). The denticles point slightly proximally along the shaft. The most distal part of the seta is thin and twisted and lacks denticles. A terminal pore was not seen.

Type 3. Peripheral setae (PS, Figs. 2C and 3B). Distribution: At the periphery of groups consisting of the much longer, straight serrate setae (Fig. 3B). Dimensions: Length ca. 100 μm ; base diameter 6 to 8 μm . Morphology: Both Figs. 2C and 3B are from *Petrolisthes cinctipes*, but peripheral setae in *P. cabrilloi* were identical. The rather indistinct annulus is located about halfway towards the tip (Fig. 2C). Postannularly the shaft carries a ventral row of denticles, which decrease in size towards the apex of the seta and are absent on the most distal part. These setae may have a shape reminiscent of the sickle setae, but are much smaller and have a distinct bifid tip (Fig. 2C). A terminal pore was not seen.

Type 4. Club-shaped setae (CS, Figs. 2F, 3F and 4A). Distribution: Multiple rows of these small setae extend along the inner and outer margins of the chelae on both dactylus and propodus (Figs. 3F and 4A). Dimensions: Length 20 to 30 μm ; base diameter 3 to 4 μm . Morphology: The shaft lacks ornamentation. The tip of the seta is distinctly bifid and carries a terminal pore (Fig. 3F).

Type 5. Smooth setae (SS, Figs. 2F and 3A, F). Distribution: Around the outer margins of the chela on both dactylus and propodus (Fig. 2F). Dimensions: Length ca. 100 μm ; base diameter 6 to 8 μm . Morphology: The shaft lacks cuticular ornamentations. The tip of the seta is distinctly bifid and carries a terminal pore.

Type 6. Plumose setae (PLS, Fig. 2E). Distribution: A single, isolated tuft on the ischium near the joint to the merus. Setae extending laterally. Dimensions: Variable, up to ca. 1000 μm in length. Morphology: A double row of long, serrated setules extend along the distal half of the shaft (Fig. 2E).

The chela (Che, Figs. 2D, 3A, 3F, 4A to D)

The pereopodal chela, formed by the movable dactylus and the distal part of the propodus, measures about 200 μm in width and 100 μm in height. Both chela margins are ornamented by a row of robust, tooth-shaped processes, each divided into an inner part and an outer part carrying a pore (Fig. 4). Pores are also present on the general cuticle along the inner margins of the two chela parts (Fig. 4B, from *P. cinctipes*).

Pereopod morphology in other porcellanids

Petrolisthes cinctipes (Figs. 2C, F, 3B, 4B and 5C, D): The 5th pereopods are almost identical to those in *P. cabrilloi*. But unlike the smooth-surfaced chela teeth in *P. cabrilloi*, the outer part of those in *P. cinctipes* have slightly serrate edges and pores guarded by small spines

(Fig. 4B). The smooth setae seem to be more twisted and the annulus more distinct than in *P. cabrilloi*.

Petrolisthes galathinus (Figs. 4C and 5E, F): The 5th pereopods are almost identical to those in *P. cabrilloi*, excepting the chelae, which bear spines on the outer parts of the tooth processes (Fig. 4C). These spines also differ from those on the chela teeth in *P. cinctipes*. Bauer (1989) provided an SEM description of the 5th pereopods in this species, with which our findings are in agreement.

Petrolisthes armatus (Fig. 6A, B): No differences were detected compared to the 5th pereopods of *P. cabrilloi*.

Pachycheles monilifer and *P. rudis* (Fig. 6C to F): The setae adorning the 5th pereopods are of the same general types as identified in *Petrolisthes cabrilloi*, but they differ somewhat in size and frequency. The sickle setae are less numerous and the straight serrate setae more numerous than in *P. cabrilloi*. In addition, the straight serrate setae are generally longer than in *P. cabrilloi*, both in absolute length and relative to the size of the pereopods.

Discussion

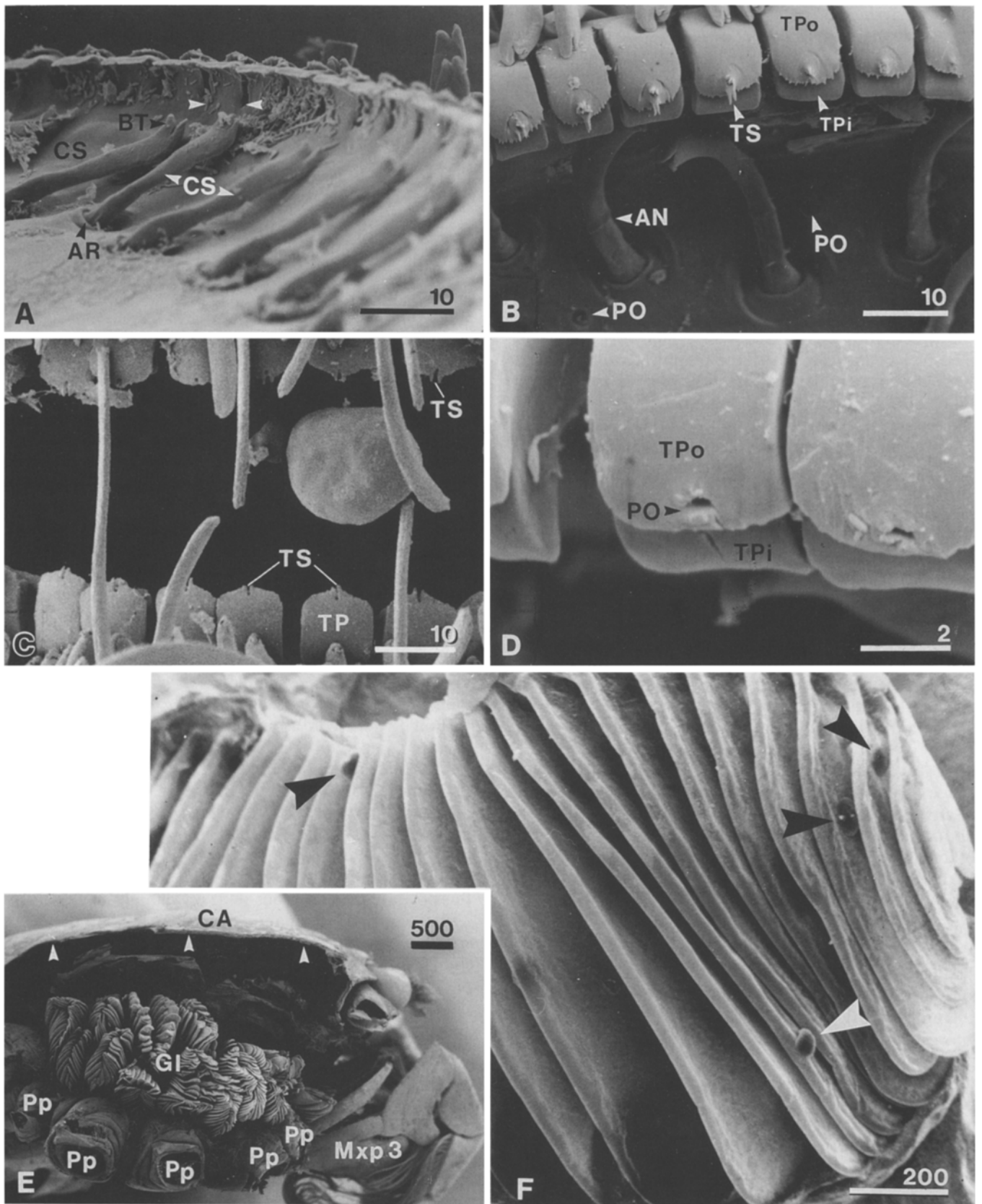
Pereopodal grooming limbs in the Anomura

The morphology of the 5th pereopodal grooming limbs was surprisingly similar among the six porcellanid species surveyed. The 5th pereopods were nearly identical in the four investigated species of *Petrolisthes*, except for a few minor details, and those in *Pachycheles* differed from *Petrolisthes* only in the frequency, distribution and detailed structure of very similar setal types and chelae ornaments.

Pohle's detailed study (1989) on body grooming shows that the 5th pereopods in *Lithodes maja* and other lithodid anomurans are in many respects comparable to those in porcellanids. Lithodids, however, carry numerous grooming setae on most limb articles, providing the entire 5th pereopod with a bottle-brush appearance. In the resting position, moreover, lithodids keep the flexed grooming limbs entirely hidden beneath the carapace. In this position the numerous setae on all limb articles act as a filter screen for inhalant water to the gills. In the more sparsely setated grooming-limb legs of porcellanids, a similar filter function could be performed by the distally placed setae and possibly also by the single tuft of plumose setae on the ischium.

There are also differences between porcellanids and lithodids in the types of setae ornamenting the grooming limbs (Pohle 1989). Lithodids seemingly lack any equivalent to the porcellanid sickle-shaped setae. Lithodid brush setae could be homologous to the straight serrate setae in porcellanids, and both types of setae predominate on the grooming limbs. Lithodid brush setae, however, are much more numerous, and their shaft carries a dense mat of very short setules and a double row of denticles, rather than two double rows of denticles and setules as in porcellanid straight serrate setae. Finally, lithodid brush setae have a bifid tip with a terminal pore.

The smooth setae in lithodids resemble those in porcellanids in both size and shape (Pohle 1989). Lithodid



smooth setae, however, are widely scattered over the limb, whereas in porcellanids they are restricted to the chela margin.

It is less certain whether porcellanid and lithodid peripheral setae are homologous, since those in lithodids carry a double row of setules rather than the single row of denticles seen in porcellanids.

The teeth along the chela margins carry a pore in both porcellanids and lithodids. Undoubtedly, these teeth are homologous and have similar functions, but unlike porcellanids, the chela teeth in *Lithodes maja* are undivided and stand in multiple rows. In addition, Pohle (1989) considered lithodid chela teeth to be true setae, although the basal articulation is hard to see in his micrographs. In porcellanids, we found no basal articulation in the teeth despite direct search.

Grooming limb motility

In porcellanids the slender limb articles connected by very flexible joints enable the 5th pereopods to reach and effectively groom most body surfaces, including the complex surfaces within the branchial chambers.

The extreme flexibility of grooming limbs is stressed by Høeg and Ritchie's (unpublished) observation for *Petrolisthes cabrilloi* of compensatory cleaning of the right gill chamber using the left grooming limb. In case of damage or complete loss of a single grooming limb, this provides an important redundancy in defending against infestation by rhizocephalan cyprids. Interestingly, Pohle (1989) found that lithodids cannot perform such compensatory cleaning.

In the Anomura, movements of the 5th pereopods inside the branchial chamber have been directly observed only in *Lithodes maja*. In this species the general sweeping over the gills consists of an antero-posterior movement of the basi-ischium and merus by flexion of the coxa-basis joint, and latero-medial movement of the carpus and chela by flexion of the merus-carpus joint (Pohle 1989). These observations and the bottle-brush morphology of the lithodid 5th pereopod also suggest that all gills in a gill chamber can be groomed with one or just a few such sweeps (Pohle 1989: Figs. 2 and 3). In species of

Petrolisthes, however, the lack of grooming setae on all but the three most distal articles most likely prohibits simultaneous grooming of all gills. We predict, therefore, that gill grooming in *Petrolisthes* spp. will turn out to be more complex, involving repeated application of the setated limb tip to each individual gill.

Grooming setae and gill grooming

The serrate setae (Type 1), sickle setae (Type 2), and peripheral setae (Type 3) are all typical grooming setae. The excellent review by Bauer (1989) showed that in the Decapoda, setae armed with two or more rows of outgrowths, denticles or setules, are common on limbs used for grooming. The denticles add significantly to the grooming efficiency by giving the setae a brush-like character. During grooming, epibiotic organisms, detritus and other kinds of debris will either stick to the setae or be scraped off the body surfaces. The straight serrate setae projecting forward both dorsally and ventrally of the chela (Figs. 2 and 5 A) can reach deep between the gill filaments while the grooming limbs makes scraping motions, and could also be responsible for cleaning the hypobranchial chamber. Pohle (1989) depicted large clumps of debris adhering to the serrated setae of the 5th pereopods as these groomed inside the gill chamber. Presumably, some debris removed by the grooming setae may also accumulate in the furrow between the denticles (Fig. 3 C, D).

The sickle-shaped seta is another adaptation which enhances grooming efficiency, either due to its scraping action or because the curved, serrated part can reach complicated and otherwise inaccessible body surfaces, such as that between individual gill filaments. There seems to be no functional reason why this type of seta is absent in lithodid crabs (Pohle 1989).

Function of the pereopodal chelae

The pereopodal chelae play a critical role in porcellanid grooming, by dealing with more firmly attached fouling objects not removed by the grooming setae. In species of *Petrolisthes*, Bauer (1989) observed how the chelae brush and pick at the gills during grooming of the branchial chambers. Situated at the tips of the flexible 5th pereopods, the chelae can reach almost everywhere inside the branchial chamber, and the teeth along the margins of the jaws assist in getting a hold on fouling objects. In *Petrolisthes* spp. the narrowly spaced gill filaments are typically only 50 µm apart (Fig. 4 E, F), but the soft, 0.5 µm thick gill cuticle (Høeg 1985) allows the rather broad chela tip to insert itself between them.

Grooming limb sensilla

The grooming limbs obviously must possess a complement of both mechano- and chemoreceptive organs in order to locate and identify fouling objects. In fact, Ache (1982) characterized pereopodal chelae as the primary

Fig. 4. *Petrolisthes* spp. (A) *P. cabrilloi*, 5th pereopod. Inner margin of terminal chela guarded by club-shaped setae (CS) with bifid tips (BT). Note lack of basal articulation (between arrowheads) in tooth processes on chela margin. (B) *P. cinctipes*. Margin and inside of terminal chela on 5th pereopod. Tooth processes split into an inner part (TPi) and an outer part (TPo) with terminal spines (TS). Pores (PO) on cuticle inside the chela. (C) *P. galathinus*. Tooth processes (TP) with terminal spines (TS) line chela margins on 5th pereopod. Round smooth object at right of center is contamination. (D) *P. cabrilloi*. Chela margin of 5th pereopod. Pore (PO) on outer part of tooth process (TPo). (E) *P. cabrilloi*. Cut carapace (arrows) revealing gills (GI) within right branchial chamber. Distal parts of pereopods 1 to 5 (Pp) removed. (F) *P. cabrilloi*. Whole gill with several kentrogons of *Lernaeodiscus porcellanae* (arrowheads) cemented to the gill filaments. Other abbreviations: AN, annulus; AR, basal articulation of seta; CA, carapace; Mxp3, 3rd maxilliped. Scale bars in µm

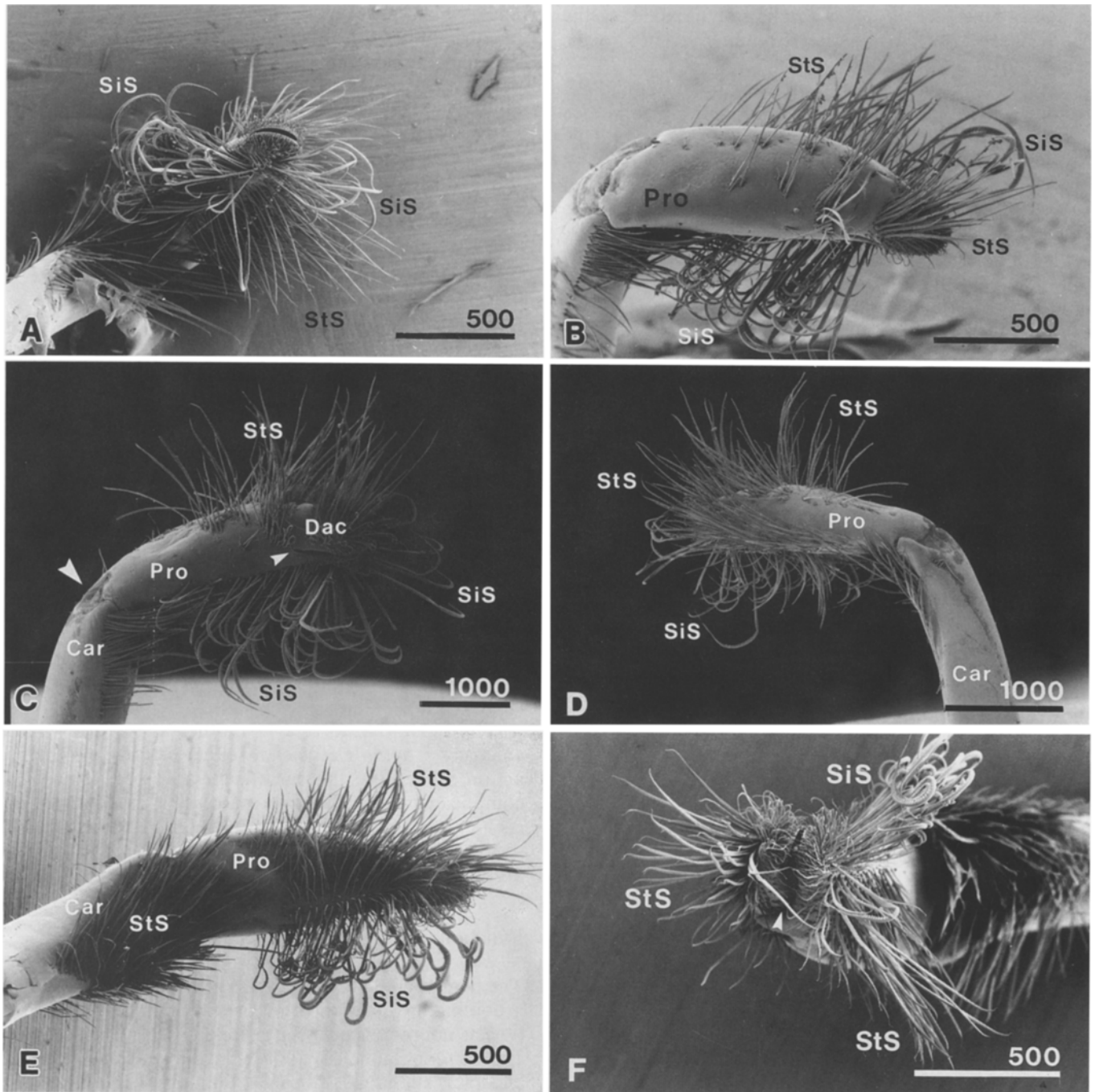


Fig. 5. *Petrolisthes* spp. Distal part of 5th pereiopod in porcelainids, showing distribution of setae. (A) *P. cabrilloi*, ventro-terminal view. (B) *P. cabrilloi*, lateral view. (C) *P. cinctipes*, lateral view. Arrowhead points to articulation between carpus and propodus. (D) *P. cinctipes*, medial view. (E) *P. galathinus*, ventral view. (F)

P. galathinus, terminal view. Arrow indicates the terminal chela. Note that all species have the numerous sickle setae (SiS) and straight serrate setae (StS) almost identically distributed on carpus (Car), propodus (Pro) and dactylus (Dac). Scale bars in μm

chemosensory organs of the Anomura, along with antennules and mouthparts. External morphology is known to be insufficient for distinguishing between mechano- and chemoreceptive setae, and bimodal receptors with both sensory properties are known to be common (Ache 1982, Schmidt and Gnatzy 1984). Watling (1989), nevertheless, offered some useful guiding principles in characterizing crustacean setae.

Mechanoreceptors

Typical mechanoreceptive setae are both annulated and setulated (Watling 1989), so the basally located, plumose setae (Type 6) likely are mechanoreceptors. Their position at the limb base near the rear inhalant opening allows them to estimate the degree of fouling in the respiratory current and initiate gill grooming if needed.

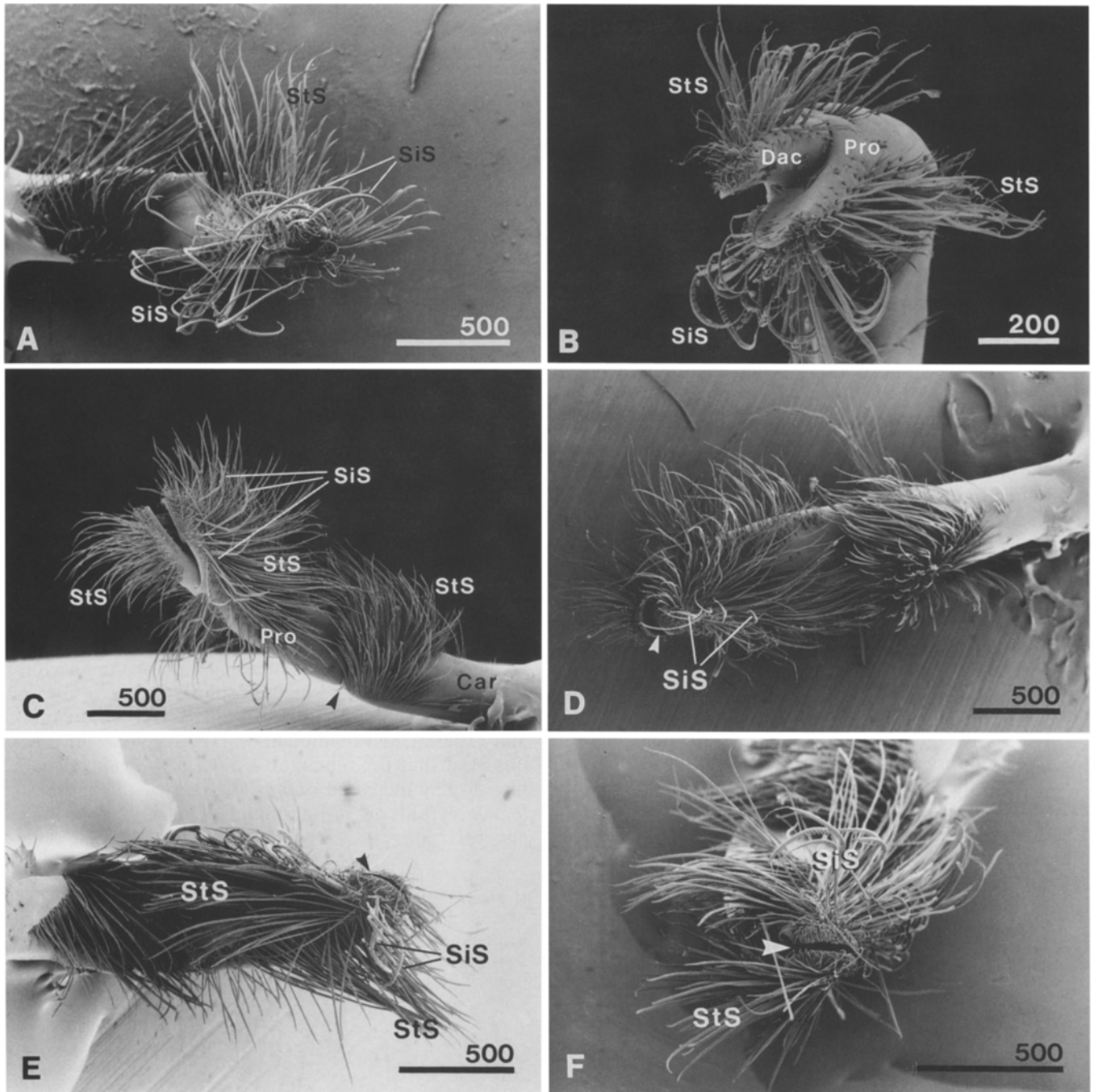


Fig. 6. *Petrolisthes armatus* and *Pachycheles* spp. Morphology of the 5th pereiopod in porcellanids. (A) *Petrolisthes armatus*, ventral view. (B) *P. armatus*, terminal view featuring the partially opened chela. (C, D) *Pachycheles monilifer*, lateral view (C) and ventral view (D). (E, F) *P. rudis*, ventral view (E) and terminal view (F).

Pachycheles species exhibit a high density of sickle setae (SiS) and straight serrate setae (StS) compared to the species of *Petrolisthes* shown here and in Fig. 5. Other abbreviations: Car, carpus; Pro, propodus. Arrowheads in (D) to (F) point to gaping margins of terminal chela. Scale bars in μm

Setae used in locating attached fouling objects obviously must be situated distally on the grooming limbs, as is the dorsal double row of setules on the straight serrate setae, which probably are mechanoreceptive. There is no evidence, however, that denticles can be mechanoreceptive (Watling 1989)

Chemoreceptors

According to the criteria of Watling (1989), the smooth setae (Type 5) and club-shaped setae (Type 4) found around the chela tip are mostly likely chemoreceptors. The hooked or twisted tips seen in the smooth setae could make objects adhere and therefore enhance stimulation of the receptor organs. The twisting is probably not an

artefact, since Bauer (1989) found similar twisted, smooth setae around the tips of the 5th pereopodal chelae in *Petrolisthes galathinus*. The pores on the inner side of the chela superficially resemble the funnel-canal organs on dactyli of the true crab *Carcinus maenas*, which Schmidt and Gnatzy (1984) showed to be bimodal receptors.

If chemosensory setae are present on the inner surface of the chela, it is likely that the porcellanids can both feel and taste objects grabbed by the pereopodal chelae during grooming. This could explain the capability observed in *P. cabrilloi* to distinguish between attached female larvae of the rhizocephalan *Lernaeodiscus porcellanae* and other fouling objects which are less direct threats (Ritchie and Høeg unpublished).

Body grooming and rhizocephalan infestation

Ritchie and Høeg (1981) and Pohle (1989) confirmed the grooming limbs' key role in maintaining the general health of the crab. Infestation by various kinds of gill parasites poses a special threat, and populations of *Petrolisthes cabrilloi* appear to be almost constantly exposed to infestation by cyprids of the rhizocephalan *Lernaeodiscus porcellanae*, which settle on and infest the gill filaments.

Soon after settlement the 220 µm long *Lernaeodiscus porcellanae* cyprid metamorphoses into a kentrogon of only 55 µm length, shaped as a smooth scale firmly cemented to the gill surface (Fig. 4F). The kentrogon, therefore, represents a much more difficult target for removal than the larger cyprid, which is attached only by two fragile antennules (Høeg 1985, Brusca and Brusca 1990). In support of this conclusion, Ritchie and Høeg (unpublished) showed that recently settled cyprids are brushed away along with miscellaneous debris during the general sweeping action of the grooming limbs, whereas kentrogons must be scraped or selectively plucked off the gill using the 5th pereopodal chela. Judging from the present study, it takes about ten chela teeth on each jaw to grip a kentrogon and pull it off. The closely spaced sensilla around the chela tip probably play a part both in locating the kentrogons and identifying them as parasite larvae.

Kentrogon removal in other porcellanid crabs

Ritchie and Høeg (1981) and Høeg and Ritchie (unpublished) showed that female cyprids of *Lernaeodiscus porcellanae* will readily settle on the gills of *Petrolisthes* species not known to host this parasite (*P. armatus*, *P. hirtipes*, and *P. gracilis*). These "non-hosts", however, were unable to remove any substantial number of kentrogons from their gills, although at least *P. armatus* and undoubtedly also *P. hirtipes* and *P. gracilis* have at their disposal grooming legs almost identical to those in *P. cabrilloi* (Figs. 4 to 6). The reason for this is that *P. cabrilloi* initiates gill grooming within seconds after introduction of *L. porcellanae* female cyprids and contin-

ues until all parasite larvae are removed, but the non-host *Petrolisthes* react much slower if at all, despite the fact that cyprids actually settle on the gills (Ritchie and Høeg unpublished). An obvious reason for this delayed response could be that the non-hosts are free from exposure to rhizocephalan infestation in their natural environment.

We conclude that the grooming limb morphology common among porcellanids evolved to deal with a variety of fouling objects. The extreme effectiveness of *Petrolisthes cabrilloi* compared to other porcellanid crabs in negating parasitism by *Lernaeodiscus porcellanae* is based, therefore, not on a specific adaptation of their grooming limbs to remove kentrogons, but rather on a combining of preexisting grooming limb morphology with behavioral adaptations, whereby this particular species recognizes its rhizocephalan parasite as a high-threat object. This is not surprising, since rhizocephalized crabs survive but are permanently sterilized, converting them into non-reproducing competitors to the healthy population.

To further elucidate these problems, a range of decapod hosts sustaining infestation by rhizocephalans should be studied with respect to grooming limb morphology and to their effectiveness in defending themselves against infestation by rhizocephalan larvae. An easy case study would be sacculinid rhizocephalans infesting brachyuran hosts, since cyprids of the Sacculinidae usually settle and metamorphose on the limbs and carapace, where they are easy objects for observations and experimental manipulation. Walker et al. (in press) observed that the blue crab *Callinectes sapidus* does in fact display increased body grooming when exposed to female cyprids of its sacculinid parasite, *Loxothylacus panopei*.

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