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## ADAPTIVE MODIFICATION OF APPENDAGES FOR GROOMING (CLEANING, ANTIFOULING) AND REPRODUCTION IN THE CRUSTACEA

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**Abstract**

Appendages used primarily for feeding and locomotion have become secondarily modified for grooming and reproductive purposes in many crustaceans. Grooming (preening, cleaning) of the body and its appendages has evolved because, particularly in marine habitats, the settling stages of microbial organisms, algae, and sessile invertebrates use the hard, nonliving exoskeleton of crustaceans as a substratum. These epibionts (fouling organisms), as well as suspended sediment and other particulate matter, may cover and impair sensory and respiratory surfaces, as well as impede limb movement and swimming efficiency. Crustaceans use specialized brushes and combs composed of setae with a complex microstructure for scraping surfaces clean. Decapod crustaceans have the best-described cleaning behavior, with gill cleaning by a variety of mechanisms necessitated by enclosure of gills in a branchial chamber. Cleaning of olfactory antennules, general body surfaces, and incubated embryos by the third maxillipeds, specialized chelae in caridean shrimps and anomuran crabs, and other pereopods is common. Other crustaceans, particularly stomatopods, some peracarids, and ostracods, groom frequently. Ablation experiments have demonstrated that deleterious fouling does occur in the absence of grooming. Some crustaceans avoid algal fouling by frequent molting, burrowing in abrasive sediments, or nocturnal behavior.

In many species, appendages have also experienced specializations for reproductive purposes. The immobile sperm of crustaceans must be actively transferred by the male in crustaceans, and a variety of appendages have become modified for this task. In various malacostracans, the first two pleopods are often modified as gonopods to either inject or deposit sperm or spermatophores in or on the female. In other crustaceans, gonopores are elaborated into papillae (penes) that insert

directly into female gonopores, or other various appendages may be modified for sperm transfer. Many male crustaceans use appendages equipped with hooks or spines to attach to females during copulation. Some very elaborate reproductive appendages might serve as courtship rather than sperm transfer devices. In many taxa, female appendages may be modified to form brood chambers to incubate embryos. The actual mechanics of reproductive appendages in crustaceans are still poorly known and remain a fertile topic for study.In most animals, appendages molded by selection for one basic function are often secondarily modified, either completely or partially, for another adaptive role. In crustaceans, two such functions are grooming (preening, cleaning) and reproduction (mating, insemination, sperm storage, incubation of embryos). Appendages or structures evolved primarily for feeding or locomotion are often later adapted for grooming or reproduction. This chapter provides an overview of grooming and sexual appendages in crustaceans, with emphasis on major morphological and phylogenetic trends in these structures. The consensus classification of Martin and Davis (2001) is used here.

## GROOMING

A major selection pressure on crustaceans, especially those in marine habitats, is fouling of body and appendage surfaces (Fig. 13.1). One major source of fouling is from particulate matter (sediment and detritus) suspended in the water column or on the substratum over which benthic organisms crawl or burrow. The other major source is the growth of other living organisms (epibionts), both microbial (e.g., bacteria, fungi, sessile protists) and macroscopic (e.g., bryozoans, hydroids, barnacles, ectoparasites), on the organism's surface. Suitable hard substrata for the settlement of both microbial and macroscopic sessile organisms are often in short supply in aquatic habitats, especially in the sea. Crustaceans are encased in a hard, nonliving, chitinous/calcareous exoskeleton with cuticular outgrowths (setae) that can be ideal sites for the accumulation of particulate matter and fouling organisms. Particles and epibionts may cover and foul respiratory surfaces (impeding gas exchange), sensory structures (preventing receptor contact with stimuli), and appendages and setae (hindering such activities as locomotion and feeding). Similar to fouling by organisms on a ship's hull, fouling on the cuticle of swimming crustaceans increases drag and decreases swimming efficiency. Although all crustaceans have a newly secreted, clean exoskeleton upon molting, significant deleterious fouling can and does occur between molts. This fouling must be removed, and most crustaceans and other arthropods have evolved behaviors for this function (Bauer 1975, 1981, 1989). Appendages and other structures used in grooming bear brushes and combs composed of complex setae (Fig. 13.2). In the many crustaceans that incubate embryos, grooming and cleaning of embryos by the female are important for successful development and hatching.

### Decapoda

*Sensory Structures*

Appendages with high concentrations of sensory structures are frequently and thoroughly cleaned by decapod crustaceans (Bauer 1989). Foremost among these are the antennules (first antennae = A1), which bear thin-walled olfactory setae or sensilla, the aesthetascs, on their outer (lateral) flagella (Hallberg and Skog 2011). Frequent A1 preening by the third maxillipeds (M3), primarily a food-handling appendage, is ubiquitous in decapods. Typically, an A1 is brought to the midline in front of the body and lowered between the outstretched M3 pair, which clamp on it with the setal grooming combs. As the A1 is raised, the M3 are lowered so that the A1 is drawn through the setal combs (Fig. 13.3A,B). Each M3 bears, on one or more of its distal articles,
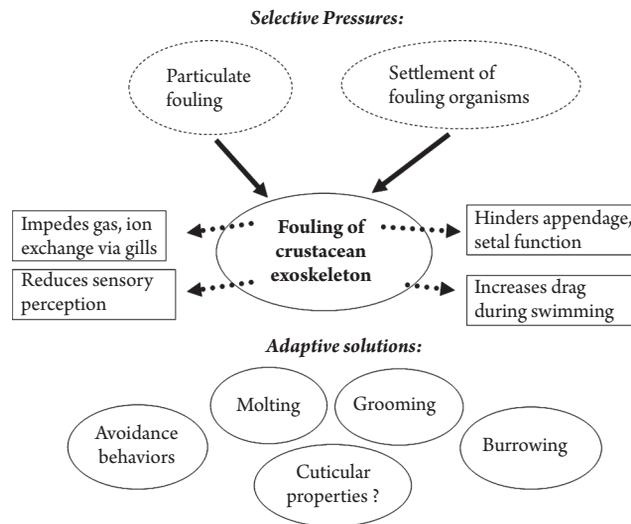
*Selective Pressures:*

Particulate fouling

Settlement of fouling organisms

Impedes gas, ion exchange via gills

Reduces sensory perception

**Fouling of crustacean exoskeleton**

Hinders appendage, setal function

Increases drag during swimming

*Adaptive solutions:*

Avoidance behaviors

Molting

Grooming

Cuticular properties ?

Burrowing

**Fig. 13.1.**
Summary of fouling pressures and adaptive solutions in Crustacea.

dense rows or combs (Fig. 13.3C) of medially placed, complex specialized setae that scrape the asthetascs and other A1 surfaces. The A1 may also be grasped and scrubbed with a rubbing action between the M3 setal combs. Each A1 cleaning seta on the M3 usually bears at least a double row of toothed branches (setules) and often bears spiny denticles or scales as well. A bout of A1 grooming is usually followed by a bout of "autogrooming" by the M3 (Fig. 13.3D). In autogrooming, limbs clean each other by rubbing against one another several times. The setal tips are oriented distally, resulting in movement of debris toward the limb tip, where it drops off.

Amputation experiments on various decapods have tested the hypothesis that A1 preening cleans the antennules and that a lack of grooming is deleterious to the animal. Bauer (1975, 1977) performed M3 ablation experiments on two caridean shrimps. The aesthetascs of the shrimp *Pandalus danae* are rather sparsely distributed on the A1 outer flagella, which are arhythmically flicked to circulate water through sensory setae. *Heptacarpus sitchensis*, on the other hand, has aesthetascs in a thick tuft on the outer flagella, which are rapidly and repeatedly spun through 180° in periodic bouts. In *P. danae*, the flagella became noticeably discolored within several days of ablation, while in *H. sitchensis* noticeable darkening occurred within two to three days, followed by obvious breakage and complete loss of the aesthetascs within 2 weeks of ablation. Flicking of the outer flagella imposes hydrodynamic forces upon the aesthetascs (Koehl 2011). Breakage of aesthetascs probably occurred in *H. sitchensis* because of the increased drag (due to fouling) on these delicate setae as they are fluttered rapidly back and forth. The fouling consisted of sediment particles, microbial growth (filamentous bacteria, diatoms, ciliates, other sessile protists), and budding colonies of fouling organisms such as bryozoans.

The second antenna (A2) flagellum of decapods is an important chemotactile appendage, and it is usually groomed. In the decapod shrimps (Penaeoidea, Sergestoidea, Caridea, Stenopodidea), the long A2 flagellum is usually cleaned by a specific pair of brushes surrounding the carpal-propodal (CP) joint of the first pereopod (P1) (Bauer 1978, De Grave and Goulding, 2011). Bauer (1978) termed these the P1–CP antennal cleaning brushes (Fig. 13.3E). The P1–CP brushes are often V-shaped and arched over the CP joint; the propodal brush is variously composed of rows of serrate setae. During A2 grooming, the shrimp reaches up with one P1 and catches the base of

**Fig. 13.2.**

Setal microstructure of grooming appendages. (A and B) Lateral and medial views of the first maxilliped grooming brushes in the stomatopod *Gonodactylus oerstedii* (modified from Bauer 1987, used with permission). (C) Serrate setae of the firth pereopod propodal grooming brush of the caridean shrimp *Pandalus danae* (from Bauer 1975, with permission from John Wiley and Sons). (D and E). Setal ultrastructure of stomatopod grooming brushes, showing multidenticulate scale setules (modified from Bauer 1987). (F) Portion of setobranch seta with multidenticulate scale setules of the caridean shrimp *Heptacarpus sitchensis* (from Bauer 1979, with permission from John Wiley and Sons). (G) Portion of seta with multidenticulate scale setule from first pereopod chela grooming brushes of the caridean shrimp *Palaemon ritteri* (from Bauer 1979, with permission from John Wiley and Sons). (H) Serrate seta of third maxilliped antennular cleaning combs of *H. sitchensis* (Bauer 2004, with permission from University of Oklahoma Press). (I and J) Grooming appendages of the ostracod *Vargula hilgendorfii* (courtesy of Jean Vannier): distal end of grooming appendage with distal terminus (t) and bristles (b) (I) and higher magnification of terminus showing small comb composed of recurved serrate setae (J).
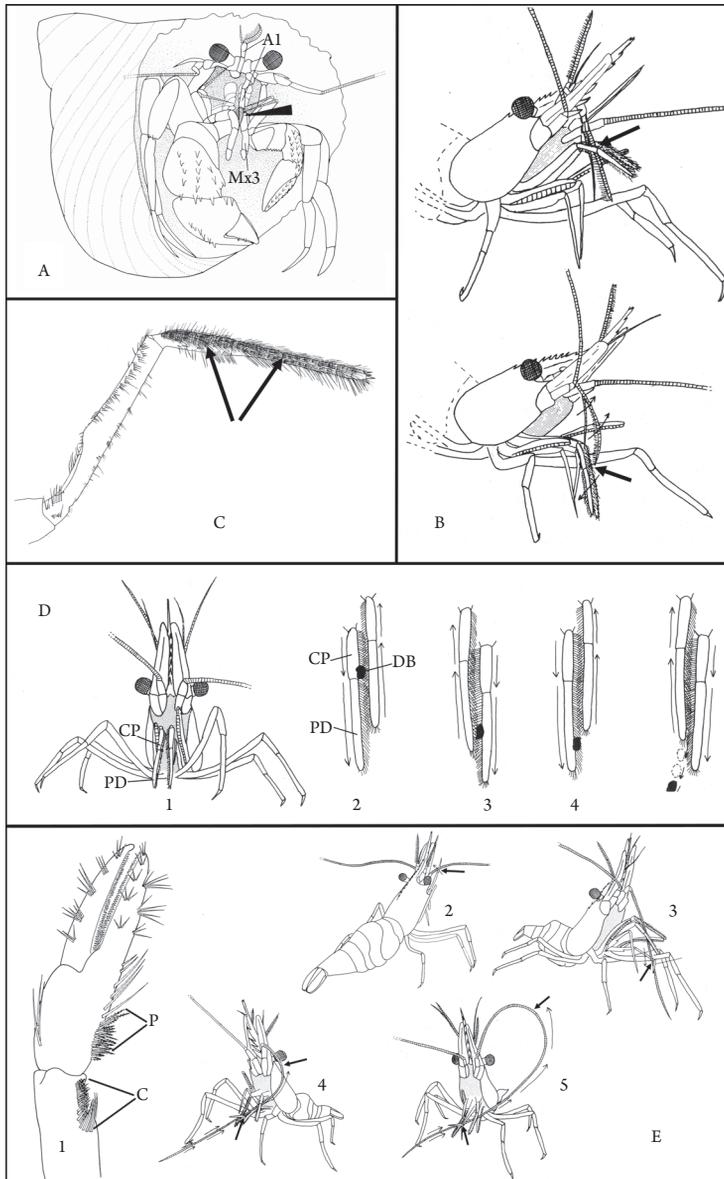
**Fig. 13.3.**
Grooming of first (A1) and second antennae. (A) The third maxillipeds (Mx3) grasp and groom an antennule (at arrowhead) in a hermit crab (from Bauer 1981, with permission from John Wiley and Sons). (B–D) Grooming in the caridean shrimp *Pandalus danae*: first antenna (B, thick arrows) grooming (thin arrows); third maxilliped, with dense rows (C, arrows) of serrate grooming setae; and third maxilliped autogrooming (D, arrows). CP, carpus; DB, debris; PD, propodus-dactylus (from Bauer 1975, with permission from Wiley Blackwell). (E) Second antenna grooming: 1, first pereopod carpal (cp) and propodal (pd) grooming brushes for second antenna (from Bauer 1981, with permission from John Wiley and Sons); 2–5, second antenna grooming by the first pereopod carpal and propodal brushes (from Bauer 1975, with permission from John Wiley and Sons).

the ipsilateral A2 flagellum between the CP brushes; the flagellum is then quickly drawn through and cleaned by the brushes (Fig. 13.3E). In other decapods, where the antennal flagellum is often shorter and/or stouter and the P1 often much larger and more robust, these brushes are not present. In such decapods, for example, astacideans, anomurans, and brachyuran crabs, the antennal flagella are simply brought between the M3, which scrub them with the serrate setae used to groom the antennules. In the stenopodidean shrimp *Stenopus hispidus*, the A1 flagella are also quite long. Interestingly, a pair of brushes surrounding the M3 propodal-dactylar joint cleans these flagella in a fashion similar to P1–CP cleaning of the A2 flagella (Bauer 1989).

### Gill Cleaning

The selective pressure to maintain clean gills and prevent their fouling is high in crustaceans, as it is in all aquatic animals. In animals without an exoskeleton, that is, fishes and soft-bodied invertebrates, epidermal tissues can secrete mucus in which sediment particles and other fouling materials are entrapped and carried off the body by ciliary currents. In crustaceans, the cuticular gills have no such autocleaning mechanism.

In decapod crustaceans, the potential for fouling of the highly branched gills is particularly great because of their enclosure within a chamber by the branchiostegite (gill cover), forming a sediment trap (Bauer 1989). Most decapods are capable of back-flushing some particulate fouling by periodic reversals of the respiratory flow ("cough reflex"). Many have a dense array of complex setae along the margins of the branchiostegite and/or the thoracic limb coxae that can filter out some particulate fouling before it enters the gill chamber. However, these setal filters cannot have too fine a mesh or they will block the respiratory flow of water. Therefore, gill fouling occurs and must be eliminated.

A variety of mechanisms have evolved in decapods to prevent or remove fouling from the gill chamber (Table 13.1) (Bauer 1981, 1989, Suzuki and McLay 1998, Batang and Suzuki 2003a, 2003b). Gill-cleaning mechanisms all involve the jostling, scraping, or brushing of complex setae (with multidenticulate, toothed, or hooked setules) among and against the gills. Gill-cleaning mechanisms might be categorized on a continuum from passive to active. Passive gill cleaning (PGC) occurs more or less automatically as the cleaning setae are jostled over and among the gills during ordinary movements of the locomotory, feeding, or respiratory structures that bear them.

One such PGC mechanism is composed of setobranchs, papillae on thoracic coxae of M3 and P1–P4 from which multidenticulate gill-cleaning setae project up into the gill chamber (Figs. 13.4A, 13.5A–D). These setobranch setae are found in many caridean shrimps, crayfishes (astacoideans, parastacoideans), and many thalassinideans (Thalassinidae, Laomedidae, Axiidae, Calocarididae). Another important PGC device is a complex of setiferous epipods on some or all of the thoracic limbs that extend up among the gills. Setiferous epipods have been described in a variety of decapods: penaeoidean shrimps (Figs. 13.4B,C, 13.5E–H) (Bauer 1999), astacideans (clawed lobsters, crayfishes) (Bauer 1998, Batang and Suzuki 2000), palinurans (e.g., spiny and slipper lobsters) (Bauer 1989), and various thalassinideans (e.g., mud lobsters, Thalassinidae; mud shrimps, Laomediidae) (Batang and Suzuki 1999, 2003, Batang et al. 2001). They are the major gill-cleaning mechanism in the "true" crabs (Brachyura) (Bauer 1989, Batang and Suzuki 2003a). In brachyurans, an epipod projecting back from the first maxilliped lies above the gills, while the epipods of the second maxilliped and M3 lie below them (Fig. 13.4D). When these maxillipeds are moved during feeding or other activities, their setose epipods are swept back and forth over the gills. In the primitive Brachyura (Dromiacea), setiferous epipods may also be present on the anterior pereopods.

Other PGC mechanisms may play a complementary or minor role in gill cleaning (Table 13.1). Long multidenticulate scaphognathite setae project backward from the posterior border of the

Table 13.1. Gill-cleaning mechanisms in decapod crustaceans reported in the literature (Bauer 1981, 1989, Suzuki and McLay 1998, Batang and Suzuki 2003a, 2003b).

| Mechanism/ Taxon | Setiferous epipods | Setobranch setae | Scaphognathite setae | | Cheliped brushing |
|---|---|---|---|---|---|
| Dendrobranchiata: | ± | – | – | ± | – |
| Penaeoidea Sergestoidea | – | – | – | – | – |
| Pleocyemata: Caridea | – | ± | ± | – | ± |
| Stenopodidea | – | – | – | – | + |
| Astacidea | ± | ± | ± | ± | – |
| Palinura | + | – | – | – | – |
| Thalassinidea | ± | ± | ± | – | ± |
| Anomura | – | – | – | – | + |
| Brachyura | + | – | ± | – | – |

Symbols: +, present; –, absent or no observations reported; ±, present in some species examined but not in others. See the text and above citations for details.

"gill bailer," or scaphognathite, the exite of the second maxilla. As the scaphognathite beats, moving water through the gill chamber, these setae simultaneously sweep over the lateral surface of the gills. In some crayfishes, the inside of the branchiostegite is studded with multidenticulate setae that project inward into the outer layer of gills (Bauer 1998, Batang and Suzuki 2000). When these podobranch gills, attached to the limb coxae, move up and down during limb movements, they are brushed by the branchiostegal setae. In the penaeid shrimp *Rimapenaeus similis*, setiferous exopods sweep over the lateral surface of the gills, cleaning them (Bauer 1999). In some of the dromiacean crabs, groups of setae arising from the body wall project into the gills and may clean them.

Although setiferous epipods, setobranchs, and branchiostegal setae are generally described as PGC, cleaning may not be entirely passive. In crayfishes (Bauer 1998, 2002, Batang and Suzuki 2000) and some carideans (Bauer 1975), there may be bouts of "limb rocking." While the animal is otherwise at rest; the pereopods are rocked to and fro. These movements, which have no other apparent function, move the setobranch setae and/or setiferous epipods within the gill chamber, presumably cleaning the gills. Similarly, the maxillipeds of brachyuran crabs may move repeatedly when the animal is at rest, but not feeding, brushing their epipods against the gills.

PGC, like active gill cleaning (see below), is very effective in keeping gill filaments clean of sediment (Fig. 13.6A,B). The sweeping action of multidenticulate scaphognathite setae, setiferous epipods, and other PGC may afford some protection against settlement of macrofouling organisms on some gill surfaces (Batang and Suzuki 2003a). However, PGC appears rather ineffective against epibiotic fouling by microbes. In experiments with the crayfish *Procambarus clarkii* and the penaeid shrimp *Rimapenaeus similis* (Bauer, 1998, 1999, respectively), microbial growth of various kinds occurred, similar to microbial fouling on ungroomed aesthetascs of the stomatopod *Gonodactylus oerstedii* (Fig. 13.7A,B). Removal of the setobranchs in *P. clarkii* from one branchial chamber but not the other resulted in significant and measurable sediment fouling on
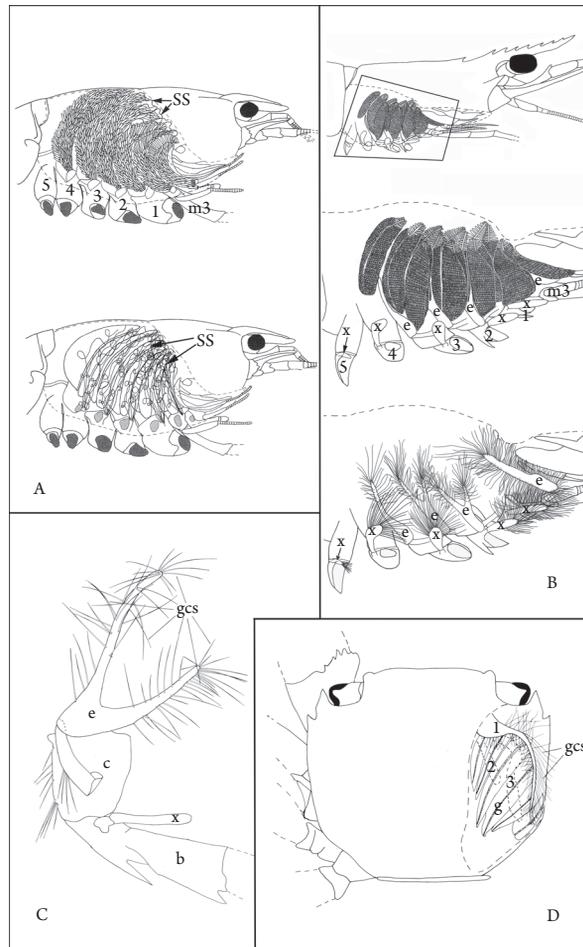
**Fig. 13.4.**
Passive gill-cleaning morphology in decapods. (A) Top, crayfish *Procambarus clarkii*, cephalothorax with gill cover removed; bottom, all gills removed to show the many setobranch setae (ss) arising from limb coxae. m3, basal segments of third maxilliped; 1–5, coxae of pereopods 1–5 (modified from Bauer 1998, his fig 1, with permission from John Wiley and Sons). (B) Penaeid shrimp *Rimapenaeus similis:* with gill cover removed to show gills (top); magnification of outlined area above, showing gills, epipods, and exopods of third maxilliped (m3) and pereopods 1–5 (middle); and with gills removed to show gill-cleaning setae on epipods (e) and exopods (x) (bottom) (from Bauer 1999, with permission from John Wiley and Sons). (C) Setiferous pereopodal epipod of the penaeid shrimp *Farfantepenaeus brevirostris.* Abbreviations: b, basis; c, coxa; e, epipod; gcs, gill-cleaning setae; x, exopod (from Bauer 1981, with permission from John Wiley and Sons). (D) Exposed right branchial chamber (dashed line) of brachyuran crab *Pachygrapsus crassipes* showing gills with epipod 1 dorsal to gills (g) and epipods 1–3 below the gills. gcs, gill-cleaning setae (from Bauer 1981, with permission from John Wiley and Sons).

most of the experimental gills (Figs. 13.6A, 13.7C,D). The lateral surfaces of the outer gills (podobranchs), which are cleaned by setae on the inside of the branchiostegite, remained clean in both the experimental and control chambers. Likewise, an inner layer of gills in the penaeoid shrimp *Rimapenaeus* was fouled when the gill-cleaning setiferous epipods were removed (Fig. 13.7E,F)
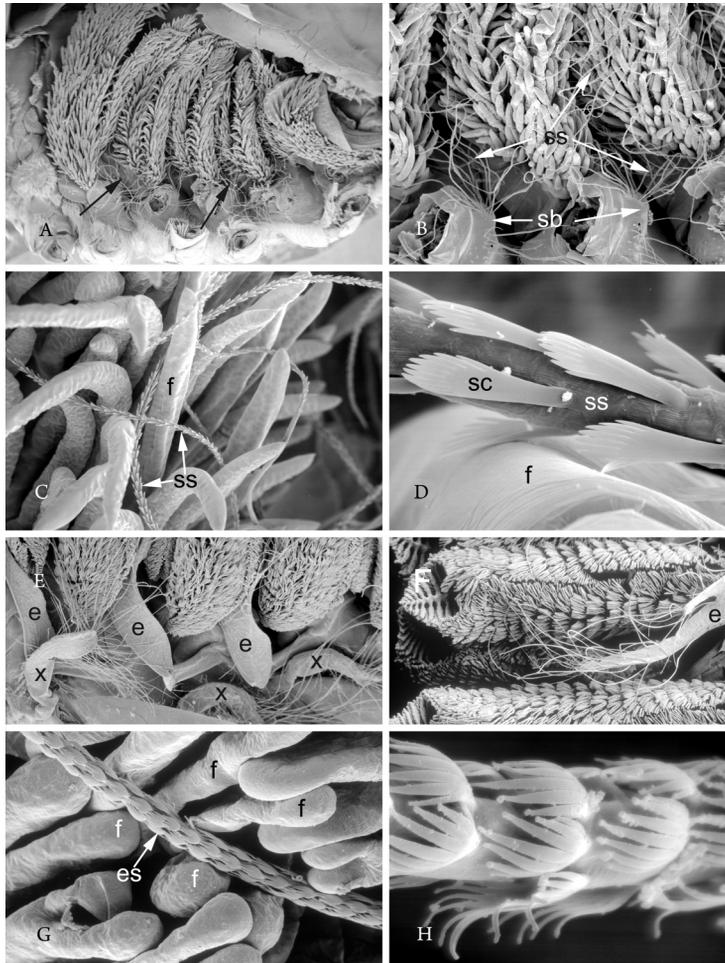
**Fig. 13.5.**
Scanning electron micrographs of passive gill-cleaning mechanisms in two decapods. (A–D) crayfish *Procambarus clarkia* (modified from Bauer 1998, with permission from John Wiley and Sons). (A) Exposed gill chamber with outer layer of gills (podobranchs) removed to show setobranch setae (arrows). (B) Coxae of pereopods with setobranchs (sb) and their setae (ss) extending up into the arthrobranch gills. (C) Setobranch setae (ss) among gill filaments (f). (D) Microstructure of setobranch setae (ss) with multidenticulate scale setules (sc) lying against a gill filament (f). (E–H) Penaeid shrimp *Rimapenaeus similis* (from Bauer 1999, with permission from John Wiley and Sons). (E) Basal segments of pereopods with the exopod (x) cleaning setae lying on gills, and proximal part of epipods (e) with cleaning setae lying between gills. (F) Tip of an epipod (e) and its setae between adjacent gills. (G) Epipod seta (es) lying among gill filaments (f). (H) Small portion of epipod seta with multidenticulate scale setules.

## Active Gill Cleaning

Other decapods lack PGC; instead, they actively brush and pick at the gills by periodically inserting grooming chelae equipped with complex setae into a gill chamber (Fig. 13.8A–D) (Bauer 1989, Pohle 1989). Grooming chelipeds in shrimps may also be used in probing the surroundings and in feeding. Cheliped brushing of gills is found in some families of caridean shrimps (Bauer
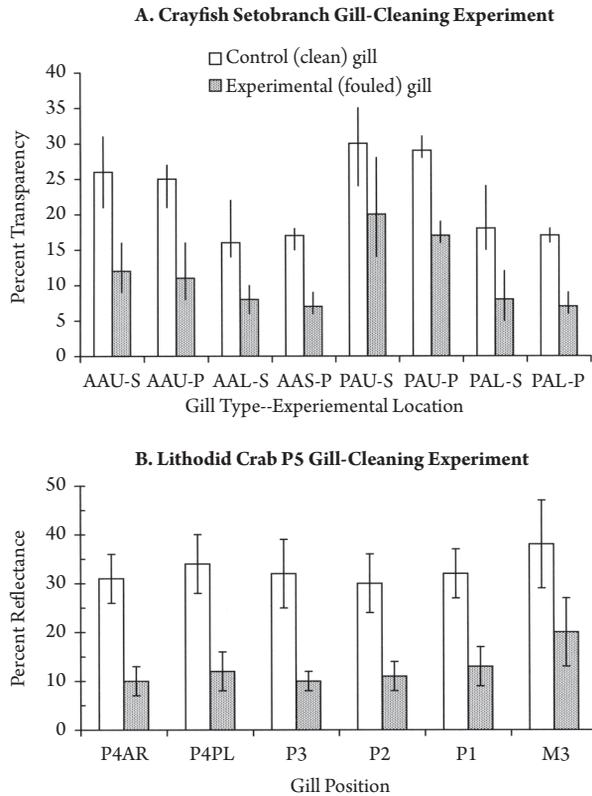
**A. Crayfish Setobranch Gill-Cleaning Experiment**



**B. Lithodid Crab P5 Gill-Cleaning Experiment**



**Fig. 13.6.**
Quantitative measures of gill fouling amputation experiments. (A) Transparency of crayfish (*Procambarus clarkii*) gills to transmitted light after exposure to fouling (medians and 95% confidence limits) (Bauer 1998, with permission from John Wiley and Sons). Control gills were in contact with setobranchs, whereas experimental gills were not. Abbreviations: AA, anterior arthrobranchs; PA, posterior arthrobranchs; L, lower half of gill; U, upper half of gill; P, commercial crayfish pond experiment; S, natural swamp experiment. (B) Light reflectance from gills of lithodid crabs with the fifth pereopod (P5) grooming limbs intact (control) or amputated (experimental) (means ± SD, from data in Pohle 1989). Abbreviations: P4AR and P4PL, arthro- and pleurobranchs of fourth pereopod; M3 and P1–P3, arthrobranchs of third maxilliped and pereopods 1–3.

1979), all anomurans, and upogebiid, callianassid, and ctenochelid thalassinideans (Bauer 1981, Batang and Suzuki 2003b). Cheliped gill brushing allows the animal to devote variable, specific time and attention to cleaning different areas of the gills, presumably stimulated by particular fouling or irritation. Gill brushing often takes a significant amount of the animal's time and energy (Bauer 1977).

In caridean shrimps, the smaller or less robust of the two pairs of chelipeds (P1 or P2, Fig. 13.8B) is usually devoted to gill and general body grooming (GBG). In addition to setal grooming brushes on the chelae, these chelipeds may have adaptations for increasing limb flexibility during grooming. In most caridean shrimps in which P2 is the gill-grooming cheliped (pandalids, hippolytids, alpheids, processids), the limb obtains increased distal flexibility by subdivision of the carpal (prechela) article into few to many articulating subunits (Figs. 13.8B, 13.9A) (Bauer 1975, 1979). The multiarticulated grooming chelipeds may be asymmetrical, in which the
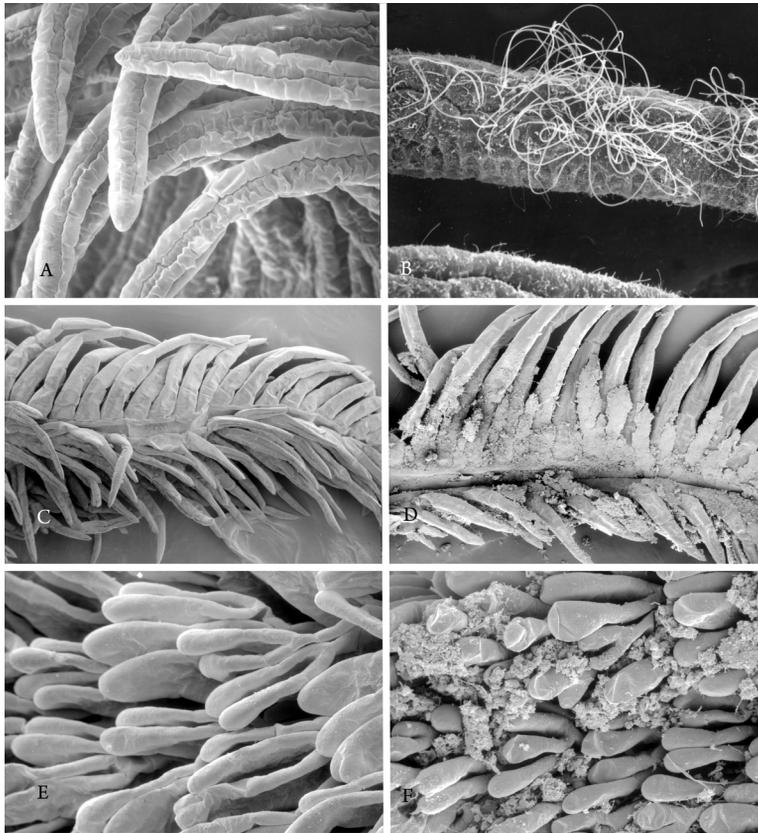
**Fig. 13.7.**
Fouling of structures by the experimentally induced absence of cleaning mechanisms. (A and B) Stomatopod *Gonodactylus oerstedii* (from Bauer 1987, used with permission): clean aesthetascs, groomed by first maxilliped (A), and aesthetascs fouled (first maxilliped removed) by filamentous bacteria (B). (C and D) Crayfish *Procambarus clarkii* (from Bauer 1998, with permission from John Wiley and Sons): clean gills (C; setobranchs present) and sediment-fouled gills (D; setobranchs removed). (E and F) Penaeid shrimp *Rimapenaeus similis* (from Bauer 1999, with permission from John Wiley and Sons): clean (E; setiferous epipods present) and fouled (F; epipods removed) gill filaments.

cheliped on one side is longer and more slender (left in pandalids, Fig. 13.9A; right in processids), with a greater number of carpal subarticles and thus more specialized for grooming (Bauer 2004). Stenopodidean shrimps also groom the gills with both the first and second chelipeds, but their grooming setae are not multidenticulate as in carideans (Bauer 1989).

Other taxa with active gill cleaning include the anomuran crabs (e.g., porcelain, sand, hermit, and king crabs; squat lobsters) and the upogebiid, callianassid, and ctenochelid thalassinideans (mud shrimps, ghost shrimps). In these decapods, it is the last pereopod (P5), usually a walking leg in other decapods, that is adapted for grooming. In anomuran crabs, the P5 is more slender and shorter than in the thalassinideans and bears a small chela, allowing them not only to brush but also to pick at small objects on the gills. In anomurans, these grooming limbs are often carried partially or completely within the gill chamber when not in use (e.g., aeglid crabs, Martin and Felgenhauer 1986; lithodid or king crabs, Pohle 1989). The P5 cleaning setae are complex and adapted for rasping, but unlike the setae used in caridean gill brushing and in PGC, their
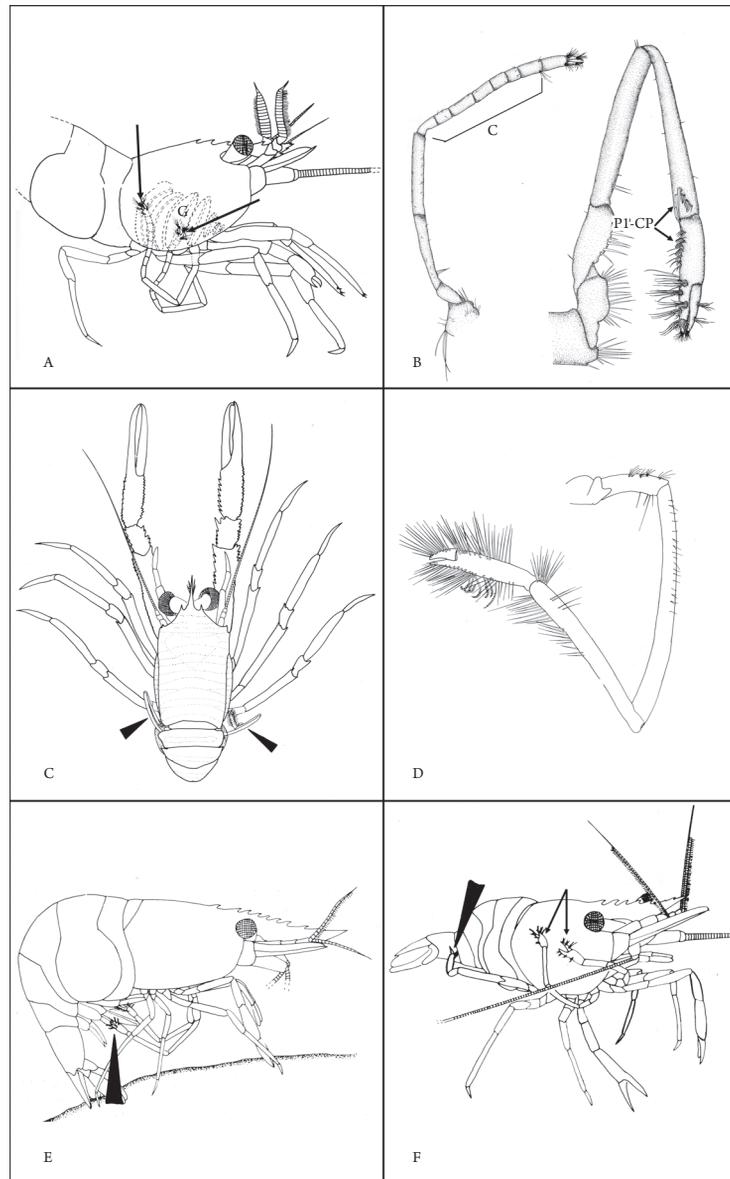
**Fig. 13.8.**
Gill and general body grooming in decapods. (A) Gill (G) cleaning by grooming chelipeds (arrows) in the caridean shrimp *Heptacarpus sitchensis* (from Bauer 1981, with permission from John Wiley and Sons). (B) Cheliped 2 (left) of *H. sitchensis*, with multiarticulated carpus (C), and cheliped 1 (right, CP) of *Palaemon ritteri*, unsegmented carpus; note the setal grooming brushes on chelae of both species and the antennal cleaning brushes on cheliped 1 of the first pereopod (P1-CP) (from Bauer 1979, with permission from John Wiley and Sons). (C) Anomuran (galatheid) crab *Pleuroncodes planipes* showing the fifth pereopod grooming appendages (arrowheads) (from Bauer 1981, with permission from John Wiley and Sons). (D) Fifth pereopod grooming appendage of the galatheid *P. planipes* (from Bauer 1981, with permission from John Wiley and Sons). (E and F) General body grooming in *P. ritteri* (from Bauer 1978, used with permission): pleopods (E) and abdomen and carapace (F).
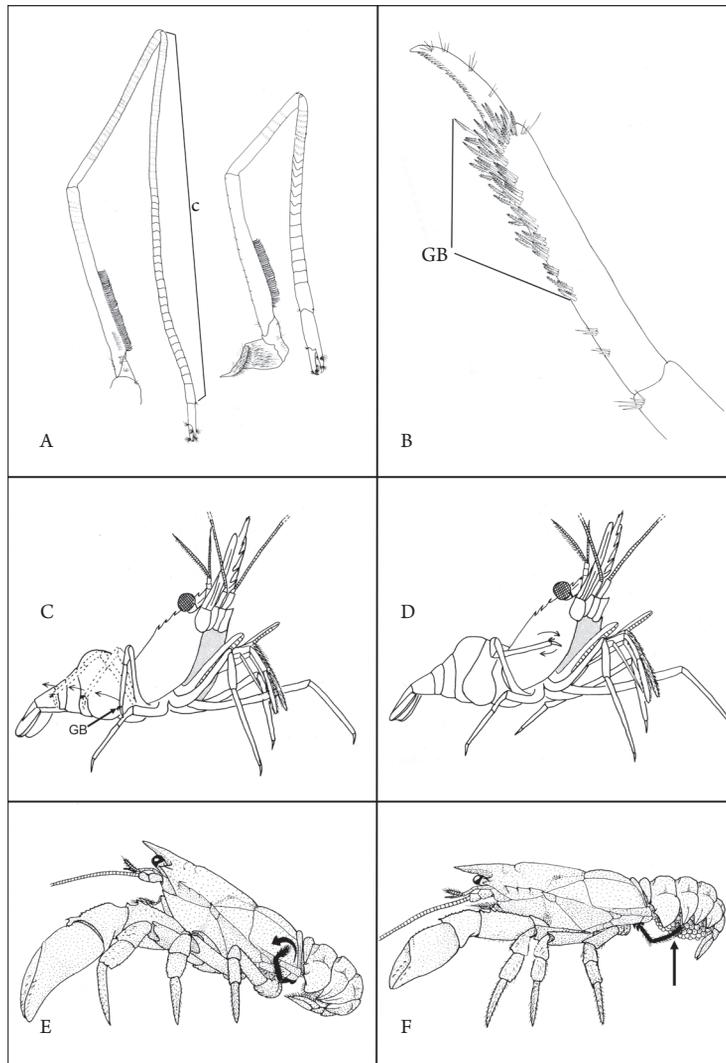
**Fig. 13.9.**
General grooming in decapod shrimps. (A) Unequal left and right second (grooming) chelipeds of *Pandalus danae*, both with multiarticulated carpus (C) (from Bauer 1975, with permission from John Wiley and Sons). (B) Distal articles of fourth pereopod of the crayfish *Procambarus clarkii* with propodal grooming brush (GB) (from Bauer 1981, with permission from John Wiley and Sons). (C) General body grooming (arrows) of the abdomen with the grooming brush (GB) (from Bauer 1975, with permission from John Wiley and Sons). (D) Carapace in *P. danae* with the fifth pereopod propodal grooming brush (from Bauer 1975). (E) Grooming of posterior carapace (arrow) (from Martin and Felgenhauer 1986, with permission from Wiley-Blackwell). (F) Incubated embryos with the fifth pereopod grooming appendage in the freshwater anomuran crab *Aegla* (from Martin and Felgenhauer 1986, with permission from Wiley-Blackwell).

ultrastructure is quite varied, for example, serrate, plumose, or smooth, but not equipped with multidenticulate scales (Pohle 1989, Fleischer et al. 1992).

Experiments in which gill-cleaning chelipeds are removed or disabled clearly show both the antifouling function and the superior effectiveness of cheliped gill brushing compared

with PGC. Bauer (1979) removed the second (grooming) chelipeds of the hippolytid caridean shrimp *Heptacarpus sitchensis* in an experimental group and the first walking legs (P3) in controls. Trauma of amputation was reduced by removing a limb at its natural basal autotomy plane, which immediately closes the wound. Within a few days of ablation, the gills of experimental shrimps became visible through the branchiostegite because of sediment fouling, while those of controls remained clean. Particulate fouling (sediment, detritus) was measured quantitatively using a light meter to record the relative transmission of light through gills mounted on slides and viewed with a light microscope (Bauer 1979). Additionally, microbial organisms (diatoms, sessile ciliates, filamentous long-chained bacteria) were found attached to gill lamellae of experimentals. Only very light epibiotic fouling occurred in controls. Shrimps with fouled gills showed distress or died in low-oxygen water, but control shrimps did not (Bauer 1979).

Pohle (1989) experimentally investigated the effectiveness of gill brushing in the anomuran crab *Lithodes maja* by either immobilizing or amputating the P5 grooming limbs. As with the caridean shrimps, heavy epizoic and sediment fouling was observed qualitatively and measured quantitatively on experimental crabs, with little fouling on control crabs (see above). Abdomens of some fouled crabs, which later died, became swollen by water uptake, possibly because of interference with ion regulation caused by gill fouling. Ritchie and Høeg (1981) showed with amputation experiments that the P5 grooming chelae of a porcelain crab are extremely effective at preventing infestation by a serious pest, a rhizocephalan barnacle, whose infective larval stages first settle on the gills.

Active gill cleaning by grooming chelipeds is clearly a more effective gill-cleaning mechanism than PGC because not only can particulate matter be brushed away but also attached epizoites can be grasped and picked off. As a result, active gill cleaning and PGC are generally mutually exclusive; decapods with grooming chelipeds have neither PGC nor branchiostegal margin or limb base setal filters. Likewise, the thalassinideans with P5 gill cleaning lack PGC present in other taxa of the group (Batang and Suzuki 2003b). All anomurans have P5 cheliped brushing but lack PGC of any kind. PGC has been shown to be the primitive and active gill cleaning the derived method of gill cleaning in decapods (Bauer 1989).

### General Body Grooming

Decapods groom their general body surfaces, including appendages and eyes, to varying degrees (Figs. 13.8E,F, 13.9B–E). In many decapods, setal brushes and combs on various appendages have evolved for GBG (Bauer 1978, 1981, 1989). In caridean shrimps, either the first or second chelipeds, whichever is the smaller, more slender pair, groom the body. In carideans with active gill grooming, the same pair of chelipeds is also used in GBG. Likewise, in anomurans, the specialized P5 chelate grooming limbs used in gill cleaning also perform GBG. In several other decapod groups, P4 and especially P5, which are nonchelate walking legs, have GBG brushes or combs of serrate grooming setae on the distal articles (Fig. 13.9B) (Bauer 1981, 1989: many caridean shrimps, astacidean crayfishes and lobsters, palinuran lobsters, thalassinideans but not dendrobranchiate and stenopodidean shrimps or brachyuran crabs). These P4 or P5 GBG brushes generally clean the abdomen and posterior cephalothorax (Fig. 13.9C–E)

The hypothesis that GBG prevents fouling of the general body surfaces has been tested experimentally. Bauer (1975, 1978) showed that marine shrimps with ablated grooming limbs suffered significant microbial (e.g., ciliate) and even macroscopic (e.g., hydroids) fouling while control shrimps did not. On the other hand, similar experiments done on freshwater crayfishes (Bauer 2002) showed little fouling when grooming was prevented. Although GBG by the minor chelipeds and last walking legs does take place in crayfishes, its frequency and duration are significantly less than in shrimps studied. Bauer (1989) showed that GBG behavior is most highly developed in

decapod shrimps such as Caridea and Stenopodidea and generally reduced or lost in the primarily benthic decapods, in which adaptations for forward swimming with pleopods and the backward escape are reduced or lost. Fouling produces drag (resistance to movement through the water), and this selective pressure is important in decapod shrimps but less so in decapods primarily adapted for crawling or running (e.g., crayfishes, lobsters, brachyuran crabs). Some anomuran crabs have highly developed GBG using the P5; they are an exception to this evolutionary trend.

### Embryo Care

Females of all decapod taxa except the dendrobranchiate shrimps incubate fertilized eggs throughout their development to hatching. After spawning and fertilization, the incipient embryos are attached to the pleopods (swimmerets) below the abdomen. Incubation includes "aeration," in which the pleopods beat or the whole abdomen flaps (brachyuran crabs) to circulate water through the embryos, facilitating oxygenation and removal of wastes from the embryos. Additionally, many decapods use grooming limbs to preen and groom the embryos. Embryo cleaning is well developed in those taxa with active gill cleaning. Thus, the stenopodidean and caridean shrimps also employ the grooming chelipeds to brush and pick among the embryos (Bauer 1979, 1981), as do decapods with P5 gill-grooming chelipeds (anomurans: Martin and Felgenhauer 1986, Förster and Baeza 2001) (Fig. 13.9F). However, minor chelipeds and/or non-chelate P5 walking legs with distal brushes and combs of some decapods (e.g., crayfishes, lobsters) can also pick at and brush the embryos, although not as efficiently as in the carideans and anomurans. Brachyuran crabs may pick and probe among the embryo mass with chelipeds (Baeza and Fernández 2002), but these limbs are usually too robust relative to embryo size to do much good and may actually cause embryo mortality.

Observations and experiments on some carideans and anomurans show that significant embryo mortality results in the absence of embryo cleaning (Bauer 1979, Pohle 1989, Förster and Baeza 2001). Buildup of sediment and detritus within the embryo mass may create anoxic areas. Bacterial growth on the embryos may prevent gas exchange and excretion (Bauer 1979); however, the deleterious effect of bacterial fouling on embryos is controversial (Kuris 1991). Small egg predators, such as nemertean worms, may infest the decapod embryo mass, causing significant embryo mortality prior to hatching. Such predators are much less prevalent in decapods using grooming chelipeds to actively clean the embryos (caridean shrimps, anomurans) than in those without such cleaning, especially the brachyuran crabs, in which high infestation and serious embryo mortality are common (Kuris and Wickham 1987).

### Other Antifouling Mechanisms

Although many decapod and other crustaceans groom frequently and intensely, others groom little or not all. Morphological specializations for grooming are not apparent in many taxa. Nonetheless, species of such taxa suffer little or no fouling. What prevents the cuticle of such crustaceans from being fouled? All crustaceans molt periodically, bestowing them with a new, unfouled exoskeleton. Molting is energetically expensive, and it is doubtful that molting rates have evolved in response to fouling. However, in many small crustaceans, frequent molting during growth may effectively eliminate the need for specific antifouling mechanisms.

Other factors may explain the low intensity or lack of grooming and their morphological specializations. Fouling pressures may vary among environments. For example, fouling pressure by macroscopic fouling organisms may be much lower in freshwater than in marine environments, given the much higher diversity of settling organisms in the latter. The lifestyle of a crustacean may impede fouling, for example, direct burrowing into mud or sand substratum (e.g., Becker and

Wahl 1996). The abrasive action of sediment particles on the exoskeleton may preclude fouling by other organisms. Consistent exposure to strong currents (high flow) may reduce fouling pressure on crustaceans (Wolff 1959). In very turbid or deep-sea environments, algal fouling pressure is absent. Isopods may be plagued by epibiotic fouling, and various mechanisms may operate to reduce this fouling, such as burrowing (Ólafsdóttir and Svavarsson 2001) or nocturnal behavior, which avoids algal fouling (Glynn 1970).

Physical and chemical characteristics of the exoskeleton surface, such as texture, surface boundary properties (e.g., hydrophilic vs. hydrophobic), and chemical defenses, may have evolved against fouling. Bauer (1981) suggested that the tegumental glands, which open onto the surface of the cuticle, could secrete antifouling compounds. However, there is no evidence of this to date. Becker and Wahl (1996) investigated the role of cuticular surface tension and bioactive compounds, which were not found to be important antifouling mechanisms in several brachyuran crabs. They concluded that behavioral activities, such as burying in sediment, aerial emersion, and nocturnal activity, were the primary antifouling mechanisms of the crabs studied. Becker et al. (2000), based on a study of fouling properties of 45 crustacean species, concluded that hydrophobic/-philic properties ("wettability") of cuticles, which might impede settlement of fouling organisms, had little relationship to fouling susceptibility.

### Grooming in Other Malacostracans

#### Stomatopoda

The stomatopods are another crustacean group in which grooming is highly developed (Bauer 1987). A single pair of specialized appendages, the first maxilliped, is adapted for grooming, with a high density and diversity of rasping and brushing setae. The first maxillipeds groom all parts of the body but concentrate, in the few species studied, on the chemosensory appendages (antennules) and the masses of gill filaments located on the pleopods (Fig. 13.10A). The unattached embryo mass is held by the maxillipeds of females in their burrows, and it is constantly kneaded and brushed during embryo development. Ablation experiments in the tropical species *Gonodactylus oerstedii* demonstrated that first maxilliped grooming protects the gills and antennular aesthetascs from microbial fouling (Bauer 1987).

#### Peracarida

Both terrestrial and aquatic amphipods (Malacostraca: Peracarida) actively groom with the first two pereopods, the subchelate (prehensile) gnathopods 1 and 2 (Caine 1976, Coleman 1989, Holmquist 1989). The distal segments of these appendages may be equipped with dense fields of multidenticulate cuticular scales or complex setae. Gnathopods brush and scrape appendages, especially the long chemosensory antennae (A1, A2). A gnathopod may individually brush the long flagellum, proximal to distal, of an A1 or A2 flagellum (Fig. 13.10B). Antennae may also be pulled to the mouthfield by a gnathopod 1, where it is cleaned by chewing of the maxillae and other mouthparts. In the Antarctic gammarid *Paraceradocus*, gnathopod 2 propodal brushes clean the uropods and pleopods by flexion of the body so that gnathopod 2 can grasp the appendage; the body is straightened out and gnathopod 2 moved forward (Coleman 1989). Gnathopods of a pair often autogroom, that is, clean each other by reciprocal rubbing. In females, incubated embryos and the ventral marsupium that contains them are brushed, cleaned, and jostled by the gnathopods.

Most isopods are also subject to epibiotic fouling (Glynn 1970, Ólafsdóttir and Svavarsson 2001). In the Isopoda (Holmquist 1989), the pereopods are cleaned by complex cuticular scales and setae of the mouthparts (mandibles, both pairs of maxillae, maxillipedal palps). A pereopod
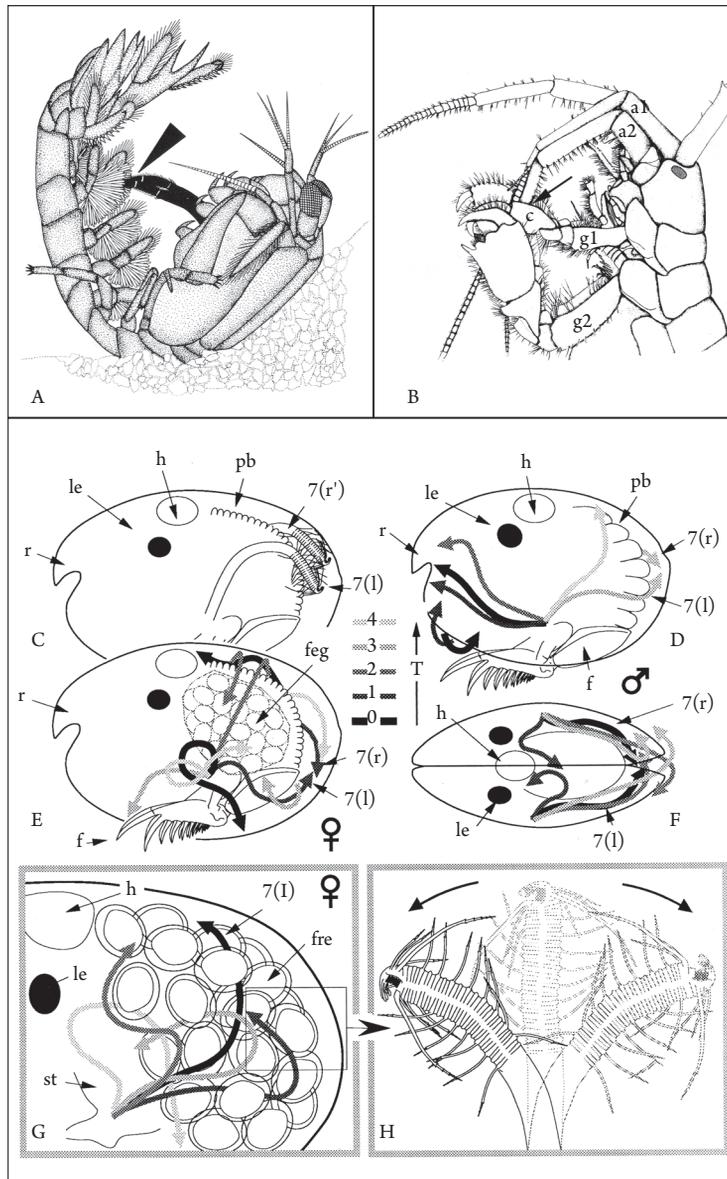
**Fig. 13.10.**
Grooming in some nondecapod crustaceans. (A) The stomatopod *Gonodactylus oerstedii* cleaning gills (arrowhead) with the first maxillipeds (black) (from Bauer 1987, with permission from John Wiley and Sons). (B) First and second antenna (a1, a2) grooming (arrow) by the first gnathopods (g1) in the gammarid amphipod *Paraceradocus gibber*. c, carpus; g2, gnathopod 2 (from Coleman 1989, used with permission). (C–H) Grooming behavior by the vermiform, multiarticulate seventh (grooming) appendage in *Vargula hilgendorfii* (from Vannier and Abe 1993, with permission from the Journal of Crustacean Biology): position of right and left seventh appendages within the shell (C), generalized grooming movements within and outside of the shell (D–F; different gray shades show time series of limb movements), grooming of embryos within the brood chamber (G), and sweeping moments by tip of grooming appendage (H). Abbreviations: f, furca; feg, fertilized eggs in ovaries; fre, embryos free within brood chamber; h, heart; le, lateral eye; pb, posterior part of body; r, rostrum; st, stomach; 7(l) and 7(r), left and right seventh appendages.

is typically brought up into the mouthparts, which grasp it; as the pereopod is withdrawn to its normal position, its distal segments are chewed and scraped by the mouthparts and their cuticular scales and setae. The P1 appears to be a major grooming appendage in isopods, with a specialized grooved carpal brush of setae, used in frequent cleaning of the A2 flagellum. Both the cleaning brush and grooming movement are very similar to P1–CP antennal brushing of decapod shrimps (Holmquist 1989); a P1 is cleaned by the mouthparts before it cleans an A2.

Mysids are shrimplike crustaceans often grouped with the peracarids primarily because females have marsupia formed by oostegites. Given their active swimming lifestyle, it is not surprising that grooming behavior may be well developed. The single in-depth study on a mysid species (Acosta and Poirrier 1992) demonstrated preening, especially of the chemosensory A1 and A2. In *Mysidopsis bahia*, the mandibular palps and thoracic endopod 2 (T2) cooperate in cleaning A1 and A2. All the other thoracic endopods, except for T1 (specialized for feeding), clean and comb their corresponding exopods, which are setose swimming structures. T8 cleans the outside, at least, of the marsupium (brood pouch); cleaning of incubated embryos was not observed. All the cleaning appendages, especially the mandibular palp and T2, are distally equipped with complex rasping or brushing setae. Paradoxically, GBG, which might be expected to be important in a swimming animal to prevent drag by epibiont fouling, was not reported.

### Grooming in Other Crustaceans

*Remipedia*

In members of the primitive class Remipedia, grooming is a frequent and noticeable behavior (Carpenter 1999, Koenemann et al. 2007). These elongate wormlike animals are composed of many similar somites with paddlelike limbs. They occur in the anchialine environment, that is, submerged caves with inland surface openings and subsurface connections to the sea (Yager 1991). The olfactory aesthetascs, located at the base of A1, are combed at each stroke of the incessantly beating pair of A2. Material groomed off the aesthetascs is directed toward the mouth and may be a form of suspension feeding on detritus. The A2 pair and the (purportedly sensory) frontal appendages periodically groom each other. The A1 flagella are periodically groomed during the forward power strokes of the anterior trunk appendages during metachronal swimming. Mouthparts (both pairs of maxillae and especially the maxillipeds) clean each other and the trunk (swimming) limbs; the posterior part of the body may be curled forward to accommodate limb grooming. Grooming becomes more frequent as remipedians are stressed during laboratory observations, especially as they are nearing death (Koenemann et al. 2007), emphasizing the importance of grooming to this crustacean. Frequent grooming in remipedes may occur in response to their constant secretion of mucus, in which particulate matter accumulates.

*Ostracoda*

This is a group of small-sized, ecologically important, diverse, and usually benthic crustaceans in which the carapace forms a bivalved shell around the body from which the appendages can be extruded. During their activities just above or within the bottom, the appendages and inside of shell may become fouled with detritus and sediment. Grooming in this class, composed of two subclasses, the Myodocopa and Podocopa, has been best summarized by Vannier and Abe (1993), with extensive observations on the myodocopid *Vargula hilgendorfii* (Fig. 13.10C–H). The last (seventh) pair of appendages are the grooming limbs in most myodocopid ostracods and are modified into long multiarticulate (vermiform), flexible limbs, very much convergent in structure and function to the multiarticulate second chelipeds described above for many caridean species. The

terminal 20 articles of the grooming limbs are equipped with setal bristles used to brush various surfaces within the shell on the appendages and, in females, the developing embryos. The terminal segments also bear a number of structures, such as combs, pegs, and hooks, which aid in scraping and rasping the body surface. This very active, flexible grooming limb may also reach outside the shell to clean its outer surfaces and appears stimulated to groom after burrowing. Grooming of embryos (Myodocopa only) appears to keep them relatively free from fouling. Embryos are also rotated by grooming, perhaps to increase water circulation among them. Vannier and Abe (1993) report that in podocopan ostracods, the seventh limb has many fewer articles and may either be a walking leg or a grooming appendage; in some ostracods, the limb is vestigial or absent.

### Branchiura

Members of the maxillopodan subclass Branchiura ("fish lice") are common ectoparasites that live on the mucus-covered bodies of fishes but that freely swim about and among hosts. Thus, it is not surprising that grooming adaptations have evolved. Martin (1932) reported that the spines and hooks of the maxillae groom the thoracopods (T1–T4), the adult swimming appendages. Additionally, Overstreet et al. (1992) reported that a posterior process (flabellum) on the exopods of T1 and T2 groom the other thoracopods. The T1 endopod bears at its tip forcepslike claws that probably clean the underside of the body.

### Mystacocarida

These tiny interstitial maxillopodans show morphological structures indicative of grooming, but this has not yet been observed (e.g., Lombardi and Ruppert's 1982 study on locomotion). Boxshall and Defaye (1996) describe a number of complex telsonic combs composed of finely digitate scale setae that, along with the pincerlike caudal furcae, might groom appendages raised toward them by flexion of the body. However, Lombardi and Ruppert (1982) hypothesized that these structures serve as important posterior contact points for the mystacocaridan's turning-escape response.

### Copepoda

Few reports on grooming have been made in the maxillopodan taxon Copepoda, indicating that it may not be a particularly frequent or important behavior in this relatively well-observed group. Costello et al. (1990) reported that the A1 of the calanoid *Centropages hamatus* is cleaned by passing it through the feeding appendages. Price et al. (1983) mentioned A1 grooming by basal segments of the maxillipeds in *Eucalanus pileatus*, as well as a rare scraping of the swimming legs by the maxillae, a behavior apparently not related to feeding. Carman and Dobbs (1997) reported microbial fouling on the body surface of copepods along with a lack of grooming and morphological specializations for it. McAllen and Hannah (1999) observed heavy microbial fouling on the harpacticoid *Tigriopus brevcornis*, which they characterized as lacking specialized grooming appendages. Biofouled individuals showed lower overall swimming rates than unfouled individuals, which might result in lower capture rates of females for mating (McAllen and Scott 2000).

### Other Crustacea

Reports and indications of grooming structures in other Crustacea are few. Many of these crustaceans are small, with rapid molting rates during most or all of their life history (e.g., copepods or most branchiopods) that may preclude grooming. Moderate or even heavy fouling may simply be tolerated, as in many branchiopods such as anostracans (D.C. Rogers, personal communication,

2011) and cladocerans, in which heavy epibiotic fouling of the carapace may increase visibility of the cladocerans to predators and clog the setal filters of the feeding appendages (Amoros 1996). Some barnacles periodically delaminate the outer layers of their calcareous shell, a possible anti-fouling adaptation (W.A. Newman, personal communication, 2011). As indicated previously, fouling pressures may be low enough in some habitats that there is little selection for specific grooming morphology and behavior. Finally, an apparent lack of grooming behavior in many crustaceans may simply be due to a lack of extensive observation of living animals.

## REPRODUCTIVE APPENDAGES AND STRUCTURES

In many crustaceans, appendages are modified for particular reproductive purposes, mainly gamete transfer and embryo incubation. Crustaceans produce sperm or eggs in gonads emptying into ducts that lead to gonopores, from which the gametes exit to the exterior. In most crustaceans, broadcast spawning of sperm and unfertilized eggs into the water, so common in many invertebrate groups, is unknown. The sperm cells are immobile (Pochon-Masson 1994) and need to be delivered by the male to the female to fertilize the eggs. In some crustaceans, insemination and fertilization are truly internal, with sperm deposited directly within the female reproductive tract (oviduct). In others, sperm deposition and subsequent fertilization are external. Sperm deposition may be internalized but not truly internal; that is, sperm or packets of sperm (spermatophores) are deposited and protected within cuticular invaginations, termed *spermathecae* (= sperm receptacles). Spermatophores may be deposited directly on or in the female by external extensions of the male ducts (genital papillae; penes) extending out from the male gonopores. However, in many crustaceans, papillae or penes cannot extend far enough to reach the appropriate location on the female. Thus, appendages with some other primary function (e.g., locomotion) may be modified or may evolve exclusively as sexual appendages for spermatophore transfer. Limbs may also be modified to incubate (brood) eggs or developing embryos. Although females of a few crustacean species release fertilized eggs into the water for development (broadcast or free spawners), most others retain and incubate the embryos during some or all of their development.

### Malacostraca

Reproductive biology of the class Malacostraca, especially the Decapoda (superorder Eucarida), has received much attention compared to that of other taxa. In all Malacostraca, the male gonopores are located on the limb coxae or the sternum of the last thoracic segment. As a result, the inner branches (endopods) of the first two abdominal appendages (pleopods) are often modified as gonopods in males to aid in transport of spermatophores to the female during copulation and insemination (Bauer 1986). In two decapod groups, the cambarid crayfishes (Astacidea) and brachyuran crabs, the endopods of the first and second pleopods (PL1, PL2) have independently evolved into a complex injection system for transferring spermatophore material into female spermathecae. An external extension of each male ejaculatory duct (genital papilla or penis) is inserted into the base of the ipsilateral, enrolled, tubelike PL1 endopod ("barrel" of the "syringe") (Fig. 13.11A) that narrows at its tip ("syringe needle"). The PL2 endopod and/or its process, the appendix masculina (AM) (Fig. 13.11B), also fits into the base of the PL1 endopod, either sealing it off or serving as a "syringe plunger," or both. Seminal material from the penes is injected with thrusting movements through the PL1 endopod into the female seminal receptacles (Andrews 1911, Hartnoll 1975, Beninger et al. 1991, Diesel 1991). Hartnoll (1975) has proposed three evolutionary grades (Fig. 13.11A,B) in the evolution of the first and second pleopods from primitive nephropidean (lobster) to dromiacean brachyuran to a derived branchyuran injection system.
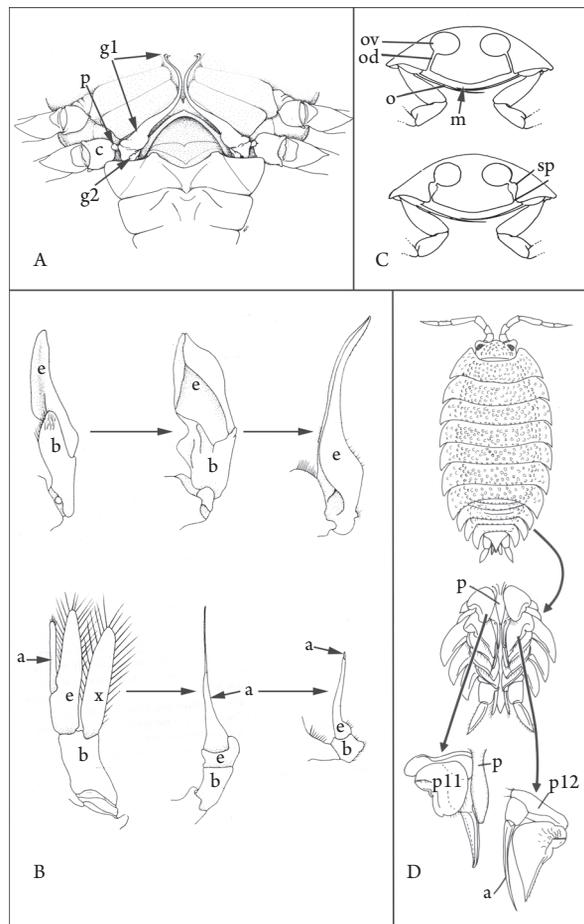
**Fig. 13.11.**
Male sperm-injection systems. (A) Ventral view of posterior thorax and anterior abdomen of a male crab, *Chionoecetes opilio* (Brachyura), showing the syringelike insemination complex of first and second gonopods (g1, g2), with the penes (p) inserted within the bases of the first gonopods. c, coxa of posteriormost pereopod (from Beninger et al. 1991, used with permission). (B) Morphological grades of male first (above) and second (below) pleopods from a simple to complex sperm-injection system in astacidean lobster *Nephrops norvegicus* (left), the primitive brachyuran *Dromia personata* (center), and more advanced brachyuran *Carcinus maenas* (right). Abbreviations: a, appendix masculina; b, basipod of pleopod; e, endopod; x, exopod (from Hartnoll 1975, used with permission). (C) Female reproductive system in the isopods *Epipenaeon* (Bopyridae, above) and *Sphaeroma* (Oniscidae, below) from cross section of thoracic segment 6. Abbreviations: o, oostegite; od, oviduct; ov, ovary, m, marsupium; sp, spermatheca (from Wilson 1991, with permission from Columbia University Press). (D) Male insemination morphology in the oniscid isopod *Porcellio*, showing the "funnel" variation of injection system. Abbreviations: a, appendix masculina; p, fused penes; pl1, pl2, first and second pleopods (from Wilson 1991, used with permission).

In another malacostracan superorder, the Peracarida, somewhat analogous pleopodal injection systems for sperm transfer have evolved in many of the Isopoda (Wilson 1991). Isopod females may store sperm in the terminal end of the oviducts, which are elaborated into cuticle-lined spermathecae (Fig. 13.11C). In some iso pods, either one or both anterior pleopods form a funnel or other complex system serving as an extension conduit from the male genital papillae (penes) into

the female gonopores (Fig. 13.11D). In other isopods, the PL2 bears a stalklike AM whose exact role in sperm transfer is unknown. Interestingly, in other members of the diverse Peracarida (e.g., mysidacean, amphipods, cumaceans, tanaidaceans), male modification of pleopods for sperm transfer is rare or absent. In these peracarids, male genital papillae may be paired or may be fused into a single genital cone or penis (Fig. 13.11D). The genital papillae or cone may simply deposit sperm near the female gonopores or elsewhere within the marsupium (female brood pouch) where spawned eggs later make contact with deposited sperm. Alternately, males may directly insert the penes into female gonopores (Wilson 1991, Johnson et al. 2001). The actual mode of insemination is rarely known with great confidence; copulation is often quite rapid, and the interplay of male and female genitalia is obstructed from view during mating.

In other malacostracans, modification of the anterior male pleopods as gonopods varies from none to complex. The PL1 endopods of males in the shrimplike anaspidacean syncarids, male euphausiaceans and dendrobranchiate decapod shrimps (penaeoideans and sergestoideans) are modified and joined to form a complex, intricate structure termed the *petasma* (Figs. 13.12A,D,F, 13.13A,B,D). As in many malacostracans, the PL2 endopods of males bear less intricate AM (Figs. 13.12C, 13.13A,C). In euphausiaceans, saclike spermatophores are attached to the female thelycum just posterior to the female gonopores under the cephalothorax. In penaeoidean and sergestoidean shrimps, single or twin sternal plates (Figs. 13.12E, 13.13E,F) comprise a "closed thelycum" behind which a single or paired spermathecae (Fig. 13.13G) are located and into which relatively simple spermatophores (Fig. 13.13H) may be deposited. Alternately, the female may have an intricately sculptured "open thelycum" (Fig. 13.12G) to which a complex external spermatophore can be attached.

Although the petasma and PL2 AMs are often referred to as "copulatory organs," their actual role in sperm transfer is problematic (Burkenroad 1934, Brinton 1978, Bauer 1991, Coineau 1996). An alternative hypothesis based on experimental work (Bauer 1996) suggested that the complex petasma serves to anchor the male in position while male genital papillae are directly inserted into the opening of female spermathecae. The species-specific petasma morphology of euphausiaceans and dendrobranchiates is suggestive of a "lock-and-key" mechanical role in copulation. However, the female thelyca of most species do not show a corresponding complex "lock" morphology to a male petasma "key." Eberhard (1985) proposed that male genitalia of many animals appear more complicated than necessary to carry out insemination. Their complexity might arise if serving as genitalic courtship devices subject to sexual selection.

In most caridean shrimps, the PL1 endopods are little to somewhat modified from a basic leaf-like swimming ramus, linked together (unlike the females) by appendices internae (Fig. 13.12B). Only in the campylonotid carideans are the PL1 endopods joined, dendrobranchiate style, all along their inner edges by cincinnuli (small curled setae) (Fig. 13.12H). The second pleopods of caridean males bear AM that vary greatly in size and shape (Bauer 2004). The role of caridean male "gonopods" in sperm transfer is controversial. Mating experiments have been conducted with caridean species (Bauer 1976, Berg and Sandifer 1984) in which males were deprived of gonopods or their rami in different combinations. In these matings, spermatophores were either not transferred or not correctly placed on the female. The model proposed was that gonopod appendices catch the adhesive spermatophores emitted by the male that were then pressed onto the female without entanglement on the male. Although the results of these studies are concordant with a hypothesis of spermatophore transfer function by PL1 and PL2, they do not reject other possible hypotheses, for example, that the gonopods are stimulating/courtship devices or perhaps sensory structures orienting the male to the female during copulation. Evidence refuting the model comes from numerous mating observations on the caridean *Lysmata wurdemanni* in which both male-phase (with AM) and simultaneous hermaphrodite (without AM) individuals are successful in mating as males (e.g., Bauer 2006).
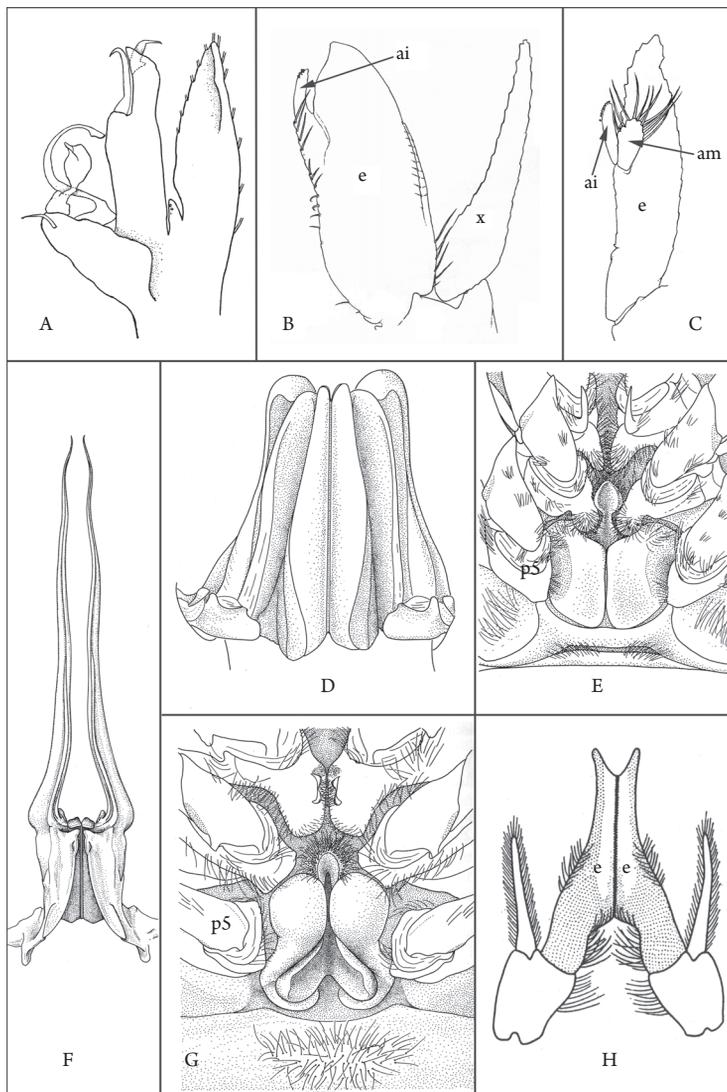
**Fig. 13.12.**
Genitalia of decapod shrimps. (A) Posterior view, right half of petasma in the euphausiid *Nematobrachion flexipes* (from Boden et al. 1955, with permission from Scripps Institution of Oceanography, UC San Diego). (B and C) Caridean *Rhynchocinetes albatrosse* (from Chace 1997, used with permission): appendix interna (ai) on the medial edge of the first pleopod endopod (e) (B) and appendices masculina (am) and interna (ai) on medial edge of the second pleopod endopod (e) (C). x, exopod. (D–G) Petasma (D, F) and closed thelycum (E, G) of the penaeid shrimp *Melicertus kerathurus* (D and E) and *Macropetasma africanus* (F and G). p5, basal articles of the fifth pereopod (from Pérez Farfante and Kensley 1997, with permission from the Muséum National d'Histoire Naturelle, Paris). (H) First pleopods of the caridean *Campylonotus vagans*, with petasma-like fusion of endopods (e) (from Torti and Boschi 1973, used with permission).

In many decapods, such as stenopodidean shrimps, parastacid and astacid crayfishes, thalassinideans, palinurid lobsters, and anomurans, the first two pleopods are only slightly, if at all, modified as apparent gonopods (Bauer 1986). One example of moderate modification is found in
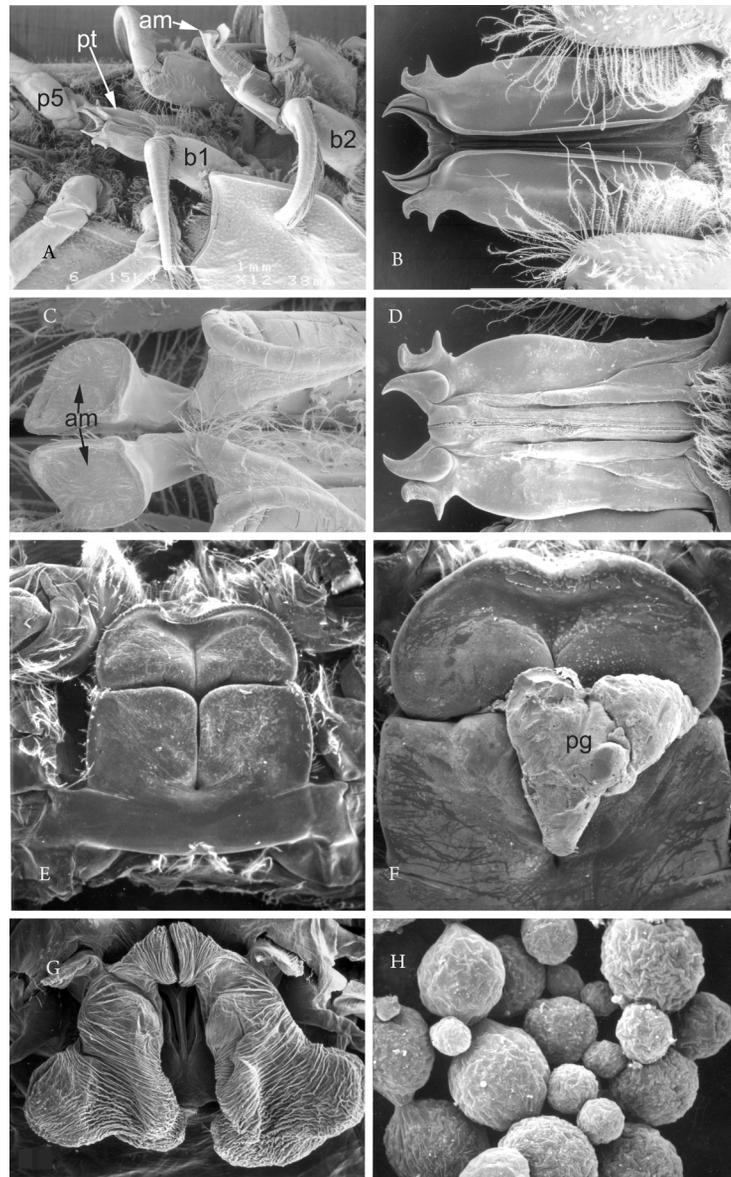
**Fig. 13.13.**
Scanning electron micrographs of penaeoid shrimp genitalia. (A–D) Male *Sicyonia dorsalis* (from Bauer 1996, with permission from Taylor and Francis, Ltd.): ventrolateral view of posterior thorax and anterior abdomen showing the petasma (pt) and appendices masculinae (am) in situ (A), petasma from posterior (ventral, B) and anterior (dorsal, D) views, and appendices masculinae (am; C). Abbreviations: b1, b2, basipods of first and second pleopods; p5, basal articles of fifth (last) pereopod. (E–H) Female *Rimapenaeus similis* (from Bauer and Min 1993, with permission from the *Biological Bulletin*): thelycum of uninseminated (E) and inseminated (F) female (with protruding male mating plug [pg]), internal view of sternum behind thelycum with baglike spermathecae (G), and sperm packets within a spermatheca (H).

galatheid crabs (Anomura), in which Kronenberger et al. (2004) hypothesized that purported male gonopods pick up a spermatophore ribbon before separation and placement of spermatophores onto the female. However, Hess and Bauer (2002) found no sperm transfer role by pleopods in the hermit crab *Clibinarius vittatus* (Anomura, Diogenidae). In some hermit and aeglid crabs (Tudge 2003), the male genital papillae are quite long ("sexual tubes") and may function in placement of spermatophores on the female during copulation (Tudge and Lemaitre 2006). In lithodid, galatheid, and aeglid crabs, the male fifth pereopods may assist in spermatophore attachment (Almerão et al. 2010). Clearly, there is much diversity in insemination mechanics that needs to be investigated in the Decapoda.

In stomatopods, appendages appear to be little modified for insemination (Caldwell 1991, Wortham-Neal 2002). The male has elongated genital papillae or penes that are inappropriately termed "gonopods" because these structures are not modified appendages. During copulation, the male inserts these penes into a genital slit on the female's sixth thoracic sternite and, via separate ducts within the penes, transmits sperm cords and secretions of accessory glands into a median seminal receptacle. The accessory gland secretion appears to be a sperm plug to prevent insemination by other males (Wortham-Neal 2002).

### Remipedia

In some crustacean classes, there is little or no modification of appendages for reproduction. The primitive wormlike, cave-dwelling remipedians are simultaneous hermaphrodites with serially homologous biramous swimming limbs. None appear modified for reproductive purposes. The male and female sexual systems are recognized externally only by placement of their respective gonopores on different trunk somites (Yager 1991).

### Cephalocarida

These small marine epibenthic crustaceans are also simultaneous hermaphrodites lacking specialized male intromittent organs (e.g., Hessler and Elofsson 1996). However, the epipods and exopods of the sixth thoracic limbs, upon whose protopods the gonopores open, are modified, possibly to concentrate or guide sperm during the presumed copulation (Hessler et al. 1995).

### Branchiopoda

This class of crustaceans with phyllopodous limbs used in locomotion and feeding has various male mechanisms for inseminating females. In the Anostraca (fairy or brine shrimps), the male gonopods, thought to be modified thoracic limbs (Rogers et al. 2007), are located just anterior to the abdomen (Fig. 13.14 A). The basic mating system of anostracans is a "scramble competition" ("pure searching") in which males constantly search for receptive females (Belk 1991). Upon encountering a female, the male interacts with her and, if allowed, grasps the female body with its two-jointed A2 around either her brood pouch or genital segment (Fig. 13.14 B) just behind her last pair of appendages (amplexial groove; Rogers 2002). One of the gonopods introduces sperm through the terminal male gonopore into the female's brood pouch via the latter's posterior pore, stimulating the release of unfertilized eggs into the brood pouch, where fertilization occurs. The A2 of male anostracans (fairy shrimps) are much larger and different in structure than those of females, often bizarrely so, with much variation among species (Belk 1991, Thiéry 1996, Dodson et al. 2010, Rogers 2002) (Fig. 13.14 C,D). In many species, the male antennal claspers form a species-specific "key" that matches the female amplexial-groove "lock" (Rogers 2002). The A2 may be
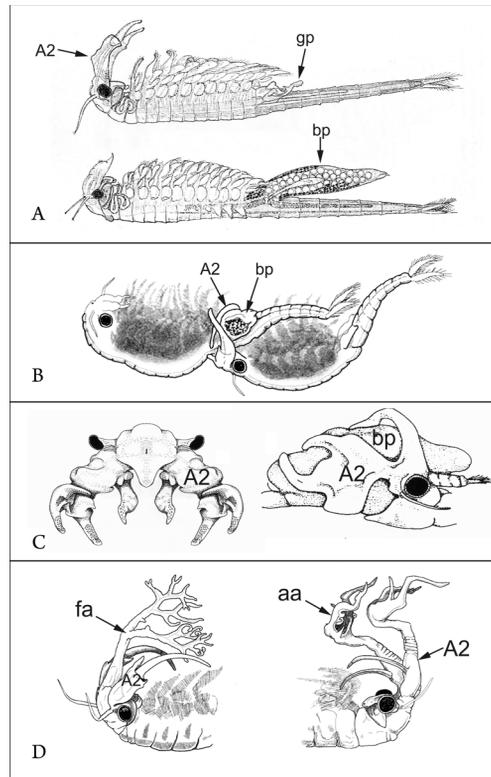
**Fig. 13.14.**
Anostracan sexual appendage morphology. (A) Male (above) and female (below) of *Branchinecta cornigera*. bp, brood pouch; gp, male gonopods (modified from Lynch 1958, used with permission). (B) Amplexus in *Linderiella occidentalis* (female at left, male at right). A2, second antenna; bp, brood pouch (modified from Dodson et al. 1958, with permission from Elsevier). (C) *Polyartemiella hazeni*: frontal (left) and lateral (right) views of male head with second antenna (A2) gripping the female brood pouch (bp) (modified from Rogers 2002, used with permission). (D) Anterior view of male *Thamnocephalus platyrus* (left) with frontal appendage (fa) and *Streptocephalus texanus* (right) with antennal appendages (aa). A2, second antenna (modified from Dodson et al. 1958, with permission from Elsevier).

Note: Please provide complete details of "Dodson et al. 1958" in the reference list.

very elaborate in structure, with a variety of surface textures, spines, knobs, and intricate antennal or frontal appendages that function as tactile premating courtship devices. Females appear to evaluate these antennal processes in choosing among males, leading Belk (1991) to the conclusion that male A2 intricacy is a result of sexual selection.

Unlike the anostracans, males of the Notostraca (tadpole shrimps) have little appendage modification for reproduction (Thiéry 1996), although male phyllopod (trunk limb) 11 serves as a male gonopod in some species. However, in another major branchiopod group, the "conchostracans" or clam shrimps (Order Diplostraca: Laevicaudata, Spinicaudata, and Cyclestherida), phyllopods 1 and 2 of males terminate in prehensile or subchelate claspers for grasping the female carapace during pairing and copulation. In the diplostracan suborder Cladocera (water fleas), the first trunk appendage of the male may similarly be prehensile or hooked for grasping the female. The A1 flagella of males in some species are elongated, with hooks and spines to aid in clinging to the female during mating (Thiéry 1996). In *Daphnia pulex*, the male seizes the female legs with T1 and long setae of A1 (Fig. 13.15A) (Dodson et al. 2010).
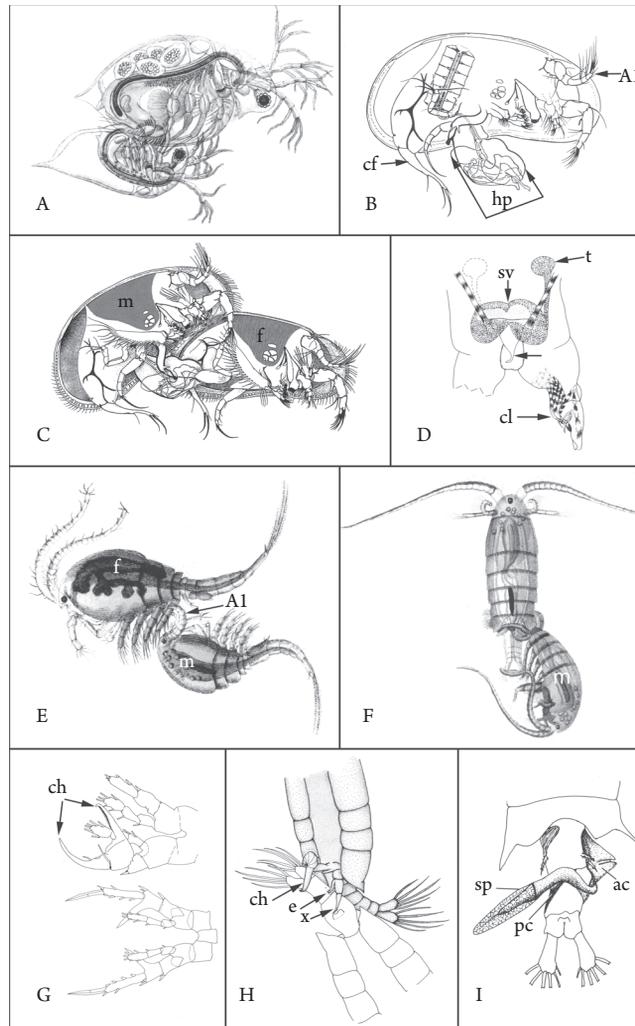
**Fig. 13.15.**

Sexual appendages and behavior of selected nondecapod crustaceans. (A) Copulation in the cladoceran *Daphnia pulex* (male below) (modified from Strickler 1998, after Jurine 1820, used with permission from the Royal Society of London). (B) Male of podocopan ostracod *Candona suburbana*, with right valve removed to show the left hemipenis rotated out in copulatory position. Abbreviations: A1, first antenna; cf, caudal furca; hp, hemipenis (modified from Morin and Cohen 1991, after McGregor and Kessling 1969, used with permission). (C) Mating of *C. suburban* male (m) and female (f) (from McGregor and Kessling 1969, used with permission). (D) Male genitalia of myodocopan ostracod *Spinacopa sandersi*. Arrow shows penis. Abbreviations: cl, clasping limb; sv, seminal vesicles; t, testis (modified from Morin and Cohen 1991, after Kornicker 1969, used with permission). (E) Mating in cyclopoid copepod *Cyclops*: male (m) grasps female (f) with both first antennae (A1) prior to copulation (modified from Strickler 1998, after Jurine 1820, used with permission from the Royal Society of London). (F) Copulation in calanoid copepod *Diaptomus*: male (m) grasps female (f) urosome with his chelate fifth swimming leg prior to spermatophore placement (modified from Strickler 1998, after Jurine 1820), used with permission from the Royal Society of London). (G) Calanoid copepod *Centropages typicus*: chelate (ch) male fifth pereopod (above) and nonchelate female fifth pereopod (below) (from Blades 1977, used with permission). (H) Copulatory position in calanoid *Labidocera aestiva*: posterior body of male (upper, stippled) and female (lower, nonstippled). The female urosome is gripped by chela (ch) of the male right fifth pereopod while the endopod (e) of the left fifth pereopod strokes female sensory pit-pore area as its exopod (x) brushes and probes her genital plate (from Blades and Youngbluth 1979, used with permission). (I) Spermatophore (sp) attached to female urosome by anterior (ac) and posterior (pc) couplers in the calanoid *C. typicus* (from Blades 1977, used with permission).

### Ostracoda

In this species-rich class, sexual morphology has been described for various species, although complementary observations on mating and copulation are relatively few. However, some generalizations can be made about the diverse reproductive appendages in the group, based primarily on the excellent reviews by McGregor and Kessling (1969) and Cohen and Morin (1990). The paired male copulatory organs, often complex and oversized in these small crustaceans, may have evolved from an eighth pair of appendages (Cohen and Morin 1990) and therefore are located just posterior to the other appendages and anterior to the caudal furcae. In the podocopans, the copulatory organs or hemipenes may be incredibly large and intricate structures (Fig. 13.15B), occupying much of the body volume. Ostracod mating appendages are sexually dimorphic, and those of males are claspers or other devices for grasping and holding the female during copulation (Fig. 13.15C). The A1 or A2 may bear suckers or hooks with which the male grasps the female (Vannier and Abe 1993). In one podocopan species, the fifth limbs are asymmetrical, with the thicker right one serving to rotate the grasped female into copulatory position (Abe and Vannier 1991). In some ostracod males, the fifth (first "thoracic") limbs have the endopod or palp modified into a pincer for holding the female carapace during copulation (McGregor and Kessling 1969). In the myodocopans, the male ducts end in a single penis situated between two variously sized and shaped copulatory or clasping organs (limbs) (Fig. 13.15D).

### Maxillopoda

Within the subclass Thecostra, the infraclass Cirripedia includes the familiar barnacles (Thoracica), ubiquitous filter-feeding sessile epifauna on hard substrata of marine environments. In these hermaphrodites, the intromittent organ of functional males is a long, remarkably mobile and flexible penis that introduces a sperm mass into the mantle cavity of another individual serving as a functional female. The penis, arising from between the bases of the posterior cirri, develops from the terminal body sclerite, which is a remnant of the larval abdomen (Walker 1992). The penis functions in precopulatory searching and copulation; no appendages are involved. A similar long penis may be present in the acrothoracicans (Klepal 1990), small cirripedes that burrow in limestone substrata, as well as in members of the infraclass Ascothoracida (Grygier 1996), free-swimming thecostrates that are endo- and ectoparasitic on coelenterates and echinoderms.

Sexual biology has been fairly well studied in two genera of the maxillopodan subclass Branchiura. In *Dolops ranarum*, the male deposits a single large spermatophore from its median gonopore; female spermathecal spines release sperm so that it flows into her spermathecal ducts (Fryer 1960). In *Argulus japonicus*, the spermathecal spines directly penetrate through the male body wall into blind ejaculatory ducts during copulation, releasing sperm that flows, driven by a pressure differential, directly into the female spermathecae (Avenant-Oldewage and Swanepoel 1993). In neither species are male appendages used to transfer sperm or spermatophores. However, in mating of *D. ranarum*, the female is initially seized by the male using its maxillulary hooks. The male then moves so as to grip the female abdomen with T2 and T3 and then presses the spermatophore against the female genital region using T4 (Fryer 1960). In *Argulus*, in addition to T2 and T3 clasping hooks and scales (setae), the male has a T4 "peg" and T3 "socket" arrangement for clasping the posterior thoracic legs of the female during copulation (Martin 1932, Avenant-Oldewage and Swanepoel 1993). Avenant-Oldewage and Swanepoel (1993) discounted earlier reports that this "peg and socket" was involved in the actual sperm transfer.

The Copepoda is a taxonomically and ecologically diverse taxon with considerable variation in morphology and mating behavior. In cyclopoids, the fifth swimming legs are rudimentary, and the male, after seizing the female with both A1 (Fig. 13.15E), simply sways its body to

the correct position next to the female for spermatophore transfer (C. Jersabek, personal communication, 2011). In the calanoids, the copepod group in which mating has been best studied (Blades-Eckelbarger 1991, Ohtsuka and Huys 2001), the major appendages modified for reproductive purposes are the male (A1) and last (thoracic) swimming leg (P5). Asymmetry of male reproductive structures is common in copepods. The right male A1 is often jointed (geniculate) and prehensile, with the segments on either side of the hinge equipped with gripping teeth and sensory setae. During mating in calanoids, the male initially grasps the female with its A1 and then swings its body around so as to seize the female with (usually) the right P5, modified for gripping the female urosome (Fig. 13.15F–H). The left P5 may first stroke and/or examine the female genital region (Blades and Youngbluth 1979). A spermatophore is then emitted from the male genital pore and attached to the genital somite of the female (Fig. 13.15I), where sperm will be discharged from the spermatophore into the female genital opening and then into the spermathecae for storage. The gripping morphology of the right P5 is quite variable but often is a large intricate chela. The left male P5 exopod is modified for seizing the spermatophore and placing it on the female, while its endopod may serve both for tactile examination of the female genital segment (Blades-Eckelbarger 1991), as well as cleaning it of debris and spermatophores from previous broods and matings (Fig. 13.15H). The fifth pereopod of females is also modified in some calanoid families to clean off discharged spermatophores, using the exopods and coxal serrations for that purpose (Ohtsuka and Huys 2001).

Tantulocarids are tiny parasites of deep-sea crustaceans that are included in the Maxillopoda in the Martin and Davis (2001) classification. The ultimate (seventh) thoracic appendages are modified into an intromittent organ or penis (Boxshall 1996). In another maxillopodan group, the mystacocaridans, small members of the interstitial fauna, there are no obvious modifications of appendages for reproduction.

## Incubatory Appendages

In many crustaceans, appendages are modified to aid incubation of brooded embryos or to help store eggs prior to fertilization and release. Embryo grooming and other incubatory activities of limbs are described above. Here, a brief review is given of appendages that form brood chambers or to which embryos are attached during incubation. Except for the dendrobranchiate shrimps, all other decapod crustaceans (suborder Pleocyemata) incubate the embryos below the abdomen until hatching. Embryos are attached to pleopods and each other to form an embryo mass. In decapods in which pleopodal swimming is reduced (e.g., lobsters, crayfishes) or absent (brachyuran crabs), the pleopods of females may function principally or only for embryo attachment. After a reproductive (parturial) molt, pleopods may undergo changes related to incubation. In caridean shrimps, for example, the protopods elongate and develop a flange that in part forms the sides of a spawning chamber that keeps fertilized eggs under the abdomen so that they can attach. The pleopod rami may have long pinnate setae that form the floor of the spawning chamber (Höglund 1943, Bauer 2004). Pleopods of reproductive female decapods bear naked "ovigerous" setae; newly spawned embryos attach to the ovigerous setae and each other to form the embryo mass that will be incubated prior to hatching.

In the malacostracan superorder Peracarida, a brood pouch (marsupium) is usually formed by medial lamellar outgrowths from the coxae, termed *oostegites*, on a variable number of thoracopods (McLaughlin 1980). Oostegite size and shape may vary greatly. In amphipods, there are two general types of oostegites. Broad oostegites with short marginal setae are characteristic of species with small eggs. In species with large eggs, a common condition in freshwater ampipods, the oostegites are narrow, with long marginal setae forming the ventral basket of the marsupium. This allows the necessary greater circulation of water around the large eggs (Steele 1991). The

latter author concluded that oostegite shape and size is more a function of environmental adaptation than ancestry. In bopyrid isopods parasitic in the gill chambers of caridean shrimps, oostegites are little to highly reduced (J. Markham, personal communication, 2011). In *Probopyrus pandalicola*, the host shrimp's gill cover functionally serves as the floor of the female isopod's marsupium; consequently, the female parasitic isopod's oostegites are highly reduced (Cash and Bauer 1993). However, in other decapod taxa with branchial bopyrids, female bopyrid oostegites are not reduced (J. Markham, personal communication, 2011). In some peracarids, the oostegites themselves are invaginated, forming individual brood pouches (Johnson and Attramadal 1982).

In the malacostracan subclass Phyllocarida (leptostracans), the bivalved carapace encloses the embryo mass for brooding. However, the endopods from the thoracic limbs of females are elongate and bear special recurved pinnate setae when a female is sexually mature, forming a bottom or floor of the brood pouch. These setae drop off after the embryos hatch, leaving basal scars (Dahl and Wägele 1996).

In the class Branchiopoda, the anostracans have lateral egg sacs that are derived from trunk limbs (D.C. Rogers, personal communication, 2011). However, their function is not to incubate embryos but rather as temporary storage for eggs in transit to the medial brood pouch in which eggs are fertilized and then later released into the environment for development. In reproductive female notostracans, the 11th trunk appendage is an oostegopod (Thiéry 1996) in which the endite is folded over to form a pouch where eggs are held until fertilization (D.C. Rogers, personal communication, 2011). In the spinicaudatan and laevicaudatan diplostracans ("conchostracans"), adhesive is secreted through exites of various trunk limbs so that fertilized eggs are glued either to appendages, the trunk, or carapace flanges (Thiéry 1996; D.C. Rogers, personal communication, 2011). In all cases, the embryo mass is enclosed by the bivalved carapace. In the Cephalocarida (*Hutchisoniella*), the two large eggs are glued for brooding to the reduced ninth thoracic legs by adhesive segmental glands (Hessler et al. 1995). Brooding of embryos may occur in other crustaceans (e.g., ostracods, copepods), but appendages are not especially modified for this purpose, except for limbs that groom brooded embryos (e.g., myodocopan ostracods).

## COMPARISONS WITH OTHER TAXA

### Grooming

Maintenance of a clean body and appendages is an important process that occurs in most animals but that has evolved under different selection pressures, resulting in somewhat different functions, depending on the group. Some animals have no appendages for cleaning and use other mechanisms to prevent or rid the body of debris. Chemical defenses are important in many sessile marine groups such as sponges and cnidarian corals. In many soft-bodied aquatic animals, frequent sloughing of surface tissues or mucus secretion prevents accumulation of fouling organisms and material. Some bryozoans and echinoderms have specialized structures for actively cleaning body surfaces free of fouling. The mucus secreted by fishes impedes fouling but is supplemented in some species by behaviors such as rubbing against the substratum or solicitation of grooming by other organisms, such as cleaner fishes and shrimps (Poulin and Grutter 1996). In birds and mammals, much time and energy may be devoted to grooming. In birds, preening maintains feather structure for flight and insulation. In mammals, fur (hair) structure must be maintained to prevent wetting and heat loss, especially in cool climates and aquatic habitats. In both groups, grooming helps keep the body free of ectoparasites, dead epidermal tissues, and other debris. In birds and especially in mammals, parent-offspring and reciprocal grooming is common, not only for the primary purposes of cleaning but also to aid with the formation of pair

bonds between both related and nonrelated individuals. Female grooming of hatched offspring may occur in crustaceans (Thiel 2007). However, reciprocal grooming between unrelated individuals is not well documented in arthropods. Reciprocity requires long-term memory of the behavior of other individuals (Wilson 2000), a trait either uncommon or unreported in arthropods, including crustaceans.

Unlike crustaceans, the other major arthropod groups, that is, the Hexapoda (insects), Myriapoda, and Arachnida, are primarily or completely terrestrial animals. However, they face fouling pressures analogous to those of crustaceans. Particulate matter suspended in air, the medium that surrounds them, is filled with dust, pollen, and spores that can foul body surfaces and appendages. Body surfaces are soiled during daily activities such as in locomotion over or in soil or other substrata, as well as during feeding. As in crustaceans, modification of appendages (mouthparts and legs: Jander 1966, Chapman 1982) for grooming (preening) has occurred as a result of these selective pressures. As in the Crustacea, the chemoreceptive antennae are the focus of much preening behavior. Antennal cleaning and limb cleaning are carried out primarily by the mouthparts, especially the mandibles and maxillae, in the more primitive insects (Jander 1966). Preening of antennae, legs, and body surfaces is an important function of the forelegs in many insects, and distal segments of these limbs are equipped with brushes, combs, and other specializations ("toilet organs") for that purpose (Hlavac 1975, Chapman 1982). General body cleaning with the legs, especially the forelegs, is common, as is mutual leg rubbing. Much of the general body preening spreads secretions (e.g., antimicrobial) of cuticular and other glands over the exoskeleton (Hlavac 1975). Such a function of general body cleaning (spreading of secretions) is unknown in Crustacea, perhaps because it has not been investigated.

Autogrooming shows striking similarities between crustaceans and insects in both behavioral and structural features. Setae in cleaning combs and brushes employed in autogrooming are similarly inclined at an angle toward the tip of the limb so that fouling material is transported distally when the two limbs of a pair are rubbed or scraped together. Collected debris is moved toward the limb tip and then drops off (Bauer 1975, 1977, Hlavac 1975). In insects, debris arriving at the end of a cleaning limb in this way is often simply rubbed off onto the substratum, a behavior not yet reported in crustaceans.

In her excellent study of grooming in insects and myriapods, Jander (1966) made generalizations about grooming that can be compared with those in Crustacea. A high frequency of grooming is correlated with high overall activity as in decapod and stomatopod crustaceans. However, whether this is simply a high frequency of grooming because all behaviors are frequent in an active animal or a real difference in the relative frequency of grooming between active versus less active species is a question that needs to be investigated.

Chelicerates (arachnids, xiphosurans, pycnogonids) have no antennae and thus no antennal grooming. Aquatic arthropods other than crustaceans, mostly the marine groups (xiphosurans or horseshoe crabs and pycnogonids) are as susceptible to epibiotic fouling as their crustacean relatives. Horseshoe crabs become heavily encrusted, especially as they grow older and intermolt periods become longer; fouling is most extensive on areas of the body (dorsal carapace) not abraded by burrowing or mating activities (Patil and Anil 2000). Prosomal limbs are relatively short and physically unable to reach the dorsal surface if they do participate in cleaning at all. The opisthomal ("abdominal") book gills clean each other without the help of prosomal appendages (Watson 1980). The usually sluggish sea spiders (Pycnogonida) are often heavily encrusted with a variety of marine epizoites such as hydroids, sponges, and tubeworms (Arnaud and Bamber 1987). Grooming is one of the functions of two appendages arising from the cephalon, the multisegmented palps and the ovigers.

The terrestrial arachnids would seem to be susceptible to similar fouling pressures as other terrestrial arthropods, but the literature on arachnid grooming is sparse, indicating that it is

not common or simply has been ignored. It is a common behavior in Opiliones (harvestmen), which use the chelate chelicerae and movable coxae of the pedipalps and forelegs (Pinto-da Rocha et al. 2007).

### Reproductive Appendages

In the aquatic arthropods, there is no broadcast spawning of sperm and egg into the water as in many aquatic invertebrates and fishes. The xiphosuran (horseshoe) crabs do release sperm over eggs spawned in depressions in moist sand high up on sandy beaches. Many terrestrial arthropods such as arachnids, myriapods, and primitive insects transfer sperm indirectly; that is, male and female genital openings are not in direct contact. With the exception of harvestmen (Opiliones) and some mites (Acari), in which males copulate with a penis, the terrestrial arachnids use indirect sperm transfer, as do many myriapods and primitive insects such as collembolans, thysanurans, and diplurans (Chapman 1982). However, in the winged (pterygote) insects, sperm transfer occurs directly by means of penes that contain the distal ends of the male reproductive tracts. Adult insects do not have well-developed abdominal appendages, but a few reduced abdominal appendages may be modified in males for grasping females (claspers) or as intromittent organs for copulation, analogous to the gonopods of crustaceans.

Although parental care of young is not common in insects in general (e.g., Tallamy 1999), when it does occur it usually takes the form of guarding the eggs or young or providing them with food. Similarly, care of embryos is common in arachnids, ranging from viviparity and care of the juveniles in scorpions to eggs sacs carried by the female in several arachnid taxa (Polis and Sisson 1990). However, there is little if any modification of appendages or other body structures for this purpose in insects and arachnids comparable to those found in crustaceans, possibly because they have much fewer appendages (usually only three or four pairs) available for modifications beyond the primary tasks (feeding and locomotion).

## FUTURE DIRECTIONS

The rather extensive work on grooming structure and function in decapod crustaceans needs to be extended to other crustacean groups. Hypotheses on the evolution of grooming behaviors can be tested by experiments with individual species as well as with the comparative method with appropriate phylogenetic adjustment (mapping of characters on phylogenetic trees to identify adaptations arising from common descent or independent evolutionary origins). The role of chemical defenses and the neuroethology of grooming are both areas that need attention, as does the role of cleaning symbioses in many crustacean groups.

The adaptive value of complex genitalia in crustaceans is as poorly known as in other animal groups. Are genitalia complex because of mechanical function in transfer or because of a courtship function (stimulation of females, sexual selection)? In many crustacean groups, even basic knowledge of mating and the mechanics of insemination is lacking. The adaptive value of appendage structures known only from taxonomic descriptions may become apparent as observation and experimentation on reproductive function is done on poorly studied taxa.

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