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THE FUNCTIONAL MORPHOLOGY OF GNATHOPODS: IMPORTANCE IN GROOMING, AND VARIATION WITH REGARD TO HABITAT, IN TALITROIDEAN AMPHIPODS

Jeff G. Holmquist

ABSTRACT

Six talitroidean amphipod species from terrestrial, semiterrestrial, fresh-water, and marine habitats were examined with scanning electron microscopy. A number of specialized and ornate grooming organs are described in which cuticular scales and setae have been modified into bristles, fans, combs, and brushes. Terrestrial, semiterrestrial, and aquatic groups possess grooming modifications quite distinct from each other, while individual species, within a single habitat group, differ much less. The structure and function of several nongrooming specializations is also discussed.

Although sexual dimorphism of arthropod grooming structures is rare, such dimorphism is present in the Amphipoda. This dimorphism stems from the use of the major grooming appendages as precopulatory organs in the male.

The cuticular structures described in this study are used to scrape and brush the body during grooming movements, presumably enabling these crustaceans to exploit better their environment.

Grooming is an important facet of crustacean life. Much of crustacean physiology and behavior is possible only through maintenance of the cuticular surface. A good discussion of potential disruptions due to cuticular fouling is given by Felgenhauer and Schram (1979). A summary of their discussion, with many additions, follows.

Respiration.—Crustaceans have a respiratory current flowing along various body parts and over the gills. These respiratory channels are an ideal location for epizoites, as these channels are often protected by the carapace or coxal plates, as in amphipods, and provide both circulating sea water and surfaces for attachment. An epizoite preference for respiratory channels is reported by Heath (1976) and Felgenhauer and Schram (1978). If fouling occurs, the efficiency of gas exchange will probably be reduced. The importance of grooming in reducing actual gill fouling has been documented by Walker (1974), Felgenhauer and Schram (1978), Bauer (1979a), and Ritchie and Høeg (1981).

Locomotion.—The major swimming appendages of many crustaceans often bear a fringe of intermeshing setae, forming "paddles." Epizoites can cause breakage of these setae and thus hinder locomotion (Felgenhauer and Schram, 1979). Bauer (1975, 1978) and Felgenhauer and Schram (1978) suggest that fouling on the body proper could increase drag and thus decrease swimming capability in shrimp. Epizoites may occlude joints and disrupt movement (Bauer, 1977; Felgenhauer and Schram, 1978).

Sensory Systems.—Location of food and discrimination between potential food items are mediated by the eyes and by chemo- and mechanoreceptors (Ache and MacMillan, 1980). If these sites are fouled, feeding could become difficult (Shelton and Laverack, 1970; Bauer, 1975, 1977). Although Shelton (1974) showed that *Crangon* can effectively find food even with algae on the aesthetascs, he also grants that chemicals probably diffuse in through the aesthetasc cuticle and that chemoreceptors are also present on other body surfaces. Felgenhauer and Schram (1979) state that chemical, vibratory, and visual stimuli might fail to evoke defensive responses, if integumentary sensory sites are fouled. Some support of this hypothesis is lent by Solon and Cobb (1980). In caridean shrimp, copulation occurs only after the female has molted; male recognition of the female's reproductive state is often via his antennal contact with her exoskeleton (Carlisle, 1962; Bauer, 1976, 1979b). Effective mating may not be possible if the aesthetascs are damaged. Sensory areas are among the most frequently groomed (Bauer, 1981), and fouling and/or damage of antennae in the absence of grooming has been reported by Snow (1973), Bauer (1975, 1977), and Felgenhauer and Schram (1978).

Water Retention.—In terrestrial crustaceans, fine granular materials may abrade articular membranes, thus causing desiccation (B. D. Valentine, unpublished observations).

Amphipods share in these crustacean woes, as they are fouled by several epizoites, particularly by peritrichous protozoans of the genus *Lagenophrys*. Studies dealing with amphipod epizoites include: Stokes (1887), Albonyi (1928), Shomay (1955), Canaris (1962), Fenchel (1965), Jakschik (1967), Scurlock (1975), Tararam *et al.* (1978), Felgenhauer (1979), and Kitron (1980). In order to combat such foulants, amphipods have evolved very intricate series of stereotyped grooming movements (Holmquist, 1981) with up to 70 distinct behavioral modes per species. The first aim of this study was to describe morphological modifications used to abet grooming behavior.

The Superfamily Talitroidea, of the Order Amphipoda, is one of the very few lower taxa of crustaceans with representatives in a variety of habitats. For instance, *Talitroides* (Family Talitridae) is a true terrestrial genus, *Orchestia* (Family Talitridae) is a semiterrestrial beach hopper, *Hyalella* (Family Hyalellidae) inhabits fresh water, and *Parhyale* (Family Hyalidae) is a marine genus. Thus, this study's second goal was to determine if morphological divergence could be attributed to differences in habitat.

MATERIALS AND METHODS

The talitroideans used in this study were taken from a variety of habitats: *Talitroides alluaudi* Chevrolat, a terrestrial species, taken from leaf litter, Flagler Beach, Florida; *Talitroides topitotum* Burt, terrestrial, in leaf litter, Grande Isle, Louisiana; *Orchestia,* new species (Bousfield, personal communication), known as the "checker-back" beach flea, semiterrestrial, among a variety of beached seaweeds, Bahia Honda, Florida Keys; *Orchestia grillus* Bosc, semiterrestrial, *Spartina* sp. bed, Ormond, Florida; *Hyalella azteca* Saussure, fresh water, in a still backwater, Olentangy River, Delaware, Ohio; *Parhyale hawaiensis* (Dana), marine, among *Enteromopha* sp. on jetty, South Padre Island, Texas. Several adult males and females of each species were examined. No intraspecific differences were noted.

The animals were fixed in 5% formalin and transferred to 70% ethanol after one week. Appendages were dissected from the amphipods, ultrasonically cleaned, air-dried, and then mounted on stubs. The stubs were sputter-coated with 200 Å gold, examined in a scanning electron microscope, and photographed on Polaroid film.

RESULTS

The first two pairs of pereopods, the gnathopods, are the only appendages used in talitroidean grooming (Holmquist, 1981) and, therefore, this discussion is confined to these appendages. A presence/absence summary of the structures found on all gnathopods examined is given in Table 1.

Table 1. Probable grooming structures on first and second gnathopods of male and female amphipods.

Structure	Gnathopod	Terrestrial				Semiterrestrial				Aquatic			
		T. alluaudi		*T. topitotum*		*Orchestia*, new species		*O. grillus*		*H. azteca*		*P. hawaiensis*	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Bristle scales	1												
	2	x	x	x	x								
Radiate scales	1					x		x					
	2						x		x				
Curved spines	1					x							
	2												
Bisected cones	1									x	x	x	x
	2										x		x
Comb scales	1									x	x		
	2										x		
Glabrate serrate setae	1									x	x	x	x
	2										x		x

Talitroides alluaudi, male.—Gnathopod 1 is relatively unmodified (Figs. 1a, 2), in an unguiform (simple) condition. The propod, carpus, and merus possess a number of stout, smooth setae, the term "smooth" taken from Thomas (1970). A few bifid setae, similar to those of *Parhyale* (Fig. 38), are also present.

Gnathopod 2 is highly modified. The propod, carpus, and merus possess pro-

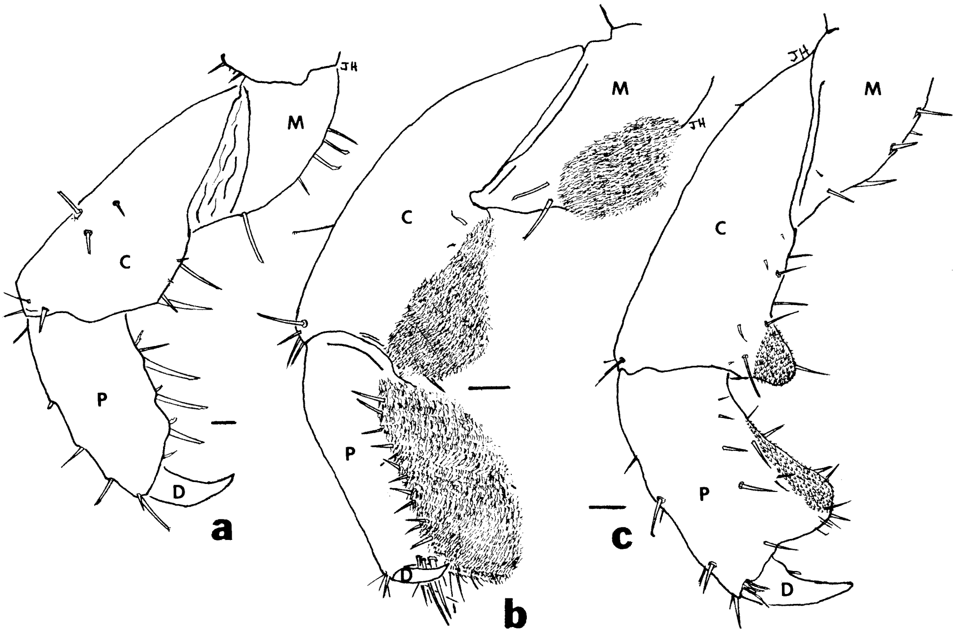


Fig. 1. a–c. C, carpus; D, dactyl; M, merus; P, propod. Bar = 50 μm. a, unguiform gnathopod 1 of female *Orchestia,* new species; b, mittenlike gnathopod 2 of female *Talitroides topitotum*; c, subchelate gnathopod 1 of male *Orchestia grillus.*

cesses (Figs. 1b, 3), each covered with a broad, echinate (set thickly with prickles) "field" of bristlelike scales (Fig. 4). In both *T. alluaudi* and *T. topitotum* these fields make up about 25% of the total surface area of the four distal segments. In addition, near the point of articulation of the dactyl and propod (Fig. 3) there are about ten setae, largely cylindrical, with vaulted plates and one flattened, imbricated (partly overlapping) side, similar to those of *Orchestia,* new species (Figs. 15, 16). A terminal pore is evident, as well as an overhanging shield. Along the margins of the echinate fields (Fig. 3) are a few setae that are quite similar to these imbricated setae with the exception of a serrate sheath extending to just proximal of the setal tip (Fig. 5). While the greater length of the sheath is actually part of the setal shaft, the most distal portion is separate from, but closely adjoins, the shaft. The former setae (Figs. 15, 16) will be referred to as imbricated setae and the latter (Fig. 5) as imbricated serrate setae.

Talitroides alluaudi, female.—The female is identical to the male, with regard to gnathopod structures.

Talitroides topitotum, male.—Gnathopod 1 is also unmodified in this species, possessing only smooth setae.

Gnathopod 2 (Fig. 1b) is similar to that of *T. alluaudi,* with echinate processes on the propod, carpus, and merus. However, unlike its congener, in which the bristle scales are arranged in large patches (Fig. 4), those of *T. topitotum* occur in small groups of two, three, or four, each group with a distinct base (Fig. 6). Also, the individual scales of *T. topitotum* are more filiform that those of *T. alluaudi* and have hooked tips. In both species, irregular rows are formed by the groups of bristle scales.

Bordering the echinate fields are 32–35 imbricated serrate setae and a few imbricated setae.

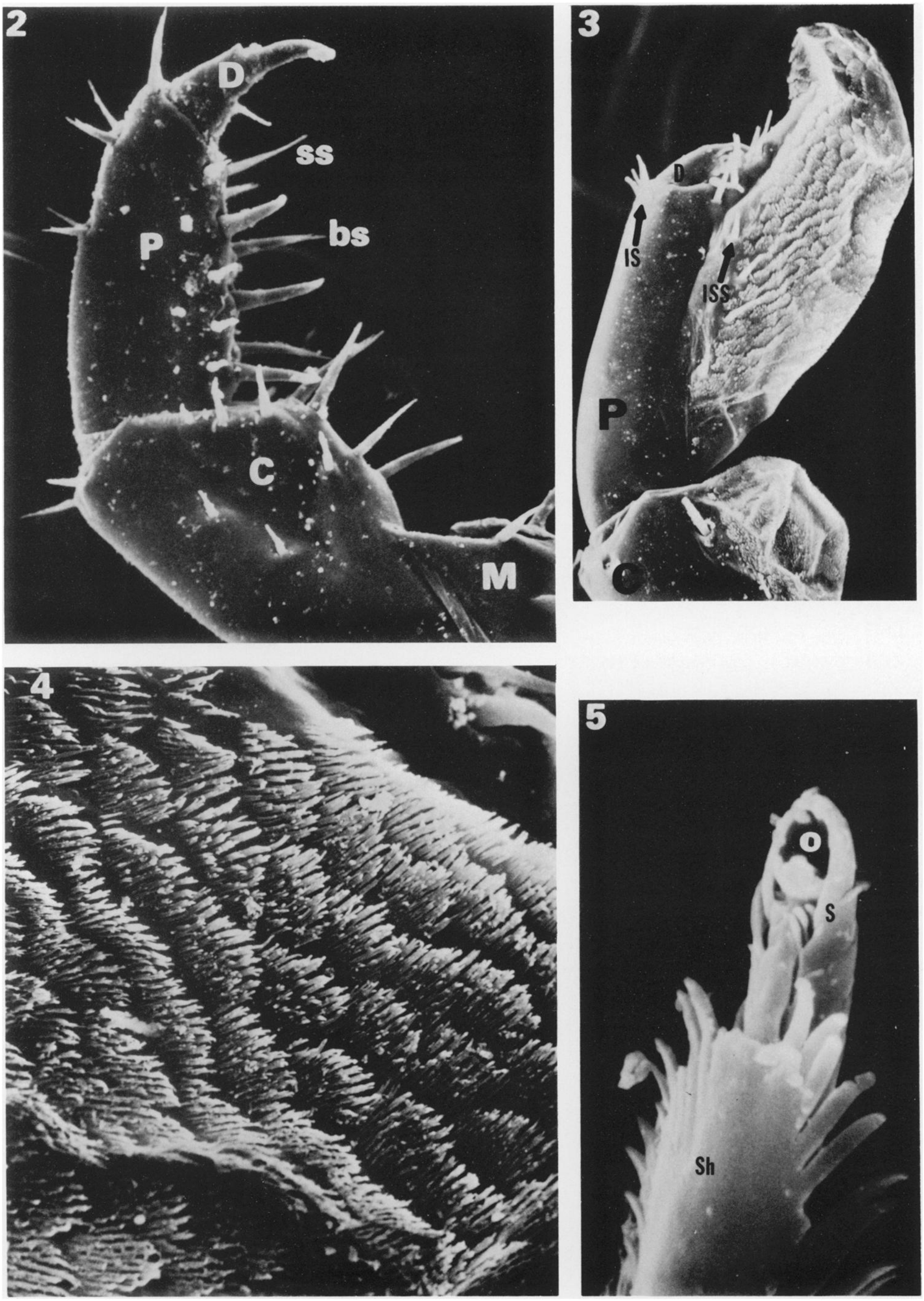
Talitroides topitotum, female.—Gnathopods are identical to those of the male.

Orchestia, new species, male.—The propod and merus of gnathopod 1 possess echinate fields composed of radiate scales (Figs. 7–10). These radiate scales are broad-based with 3–8 spinules. As a rule, smaller scales have more spinules; larger scales have fewer and broader spinules (Fig. 9). The distal dactylar surface is armed with a series of curved spines (Fig. 11). The palmar surface (the distal surface of the propod, against which the dactyl closes) is studded with subacute conical spines (Figs. 12–14).

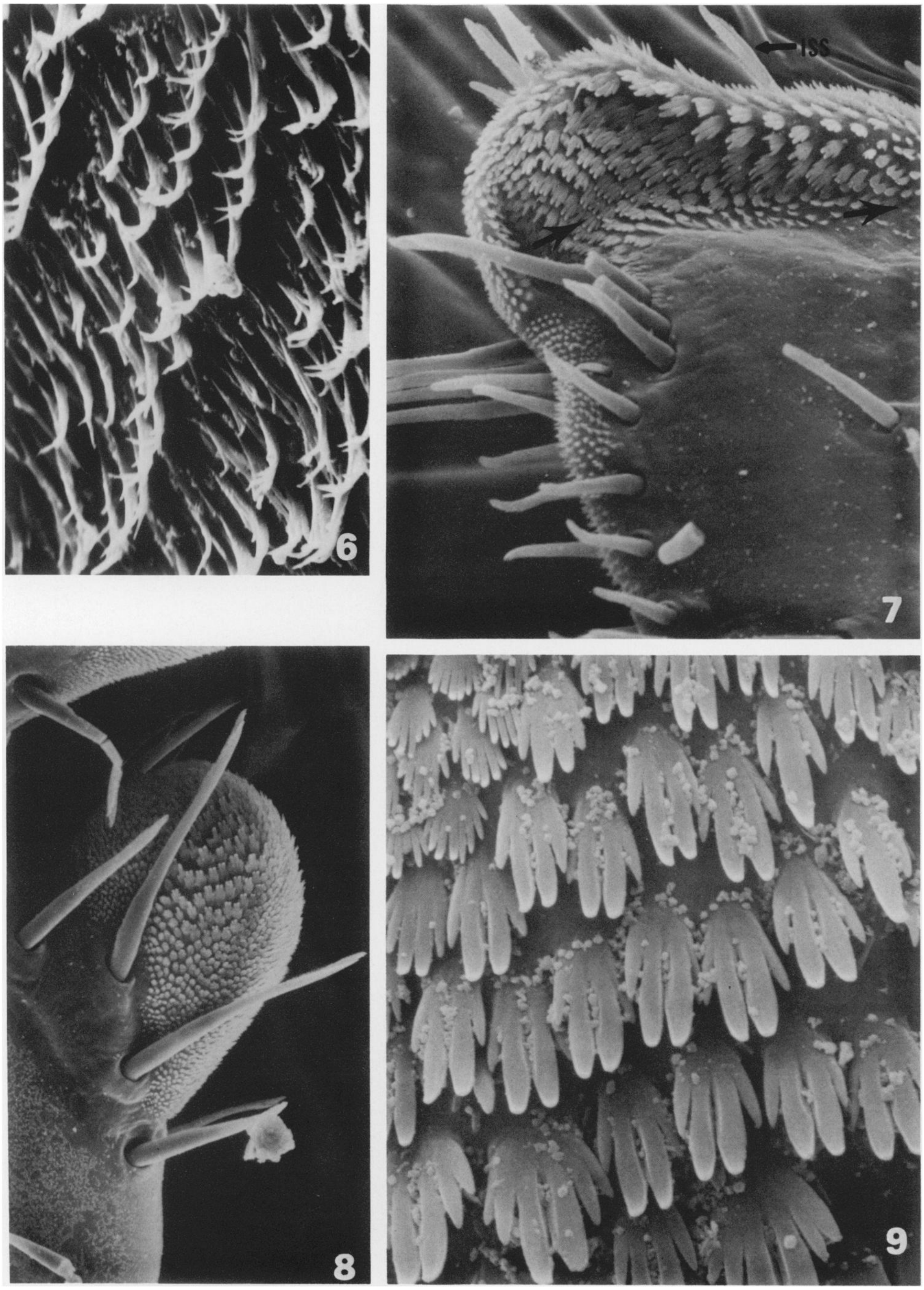
About 15 imbricated serrate setae are scattered about the edges of the propodal process (Fig. 7). Imbricated setae (~25) are present (Figs. 15, 16) on both the propod and dactyl, most of which are concentrated near the palmar surface (Figs. 12, 13). The imbricated setae are aligned on both sides of the palm, the openings of both groups arching medially towards the palm.

The male gnathopod 2 is strongly subchelate, with a coarse double row of bifid setae on the palmar surface; the rows are separated by a medial ridge. These setae are of two sizes: ~60 μm and ~25 μm, with one or two small setae regularly placed between any two of the larger (Fig. 17). Details of the dactylar and propodal surfaces are as described below for *O. grillus.*

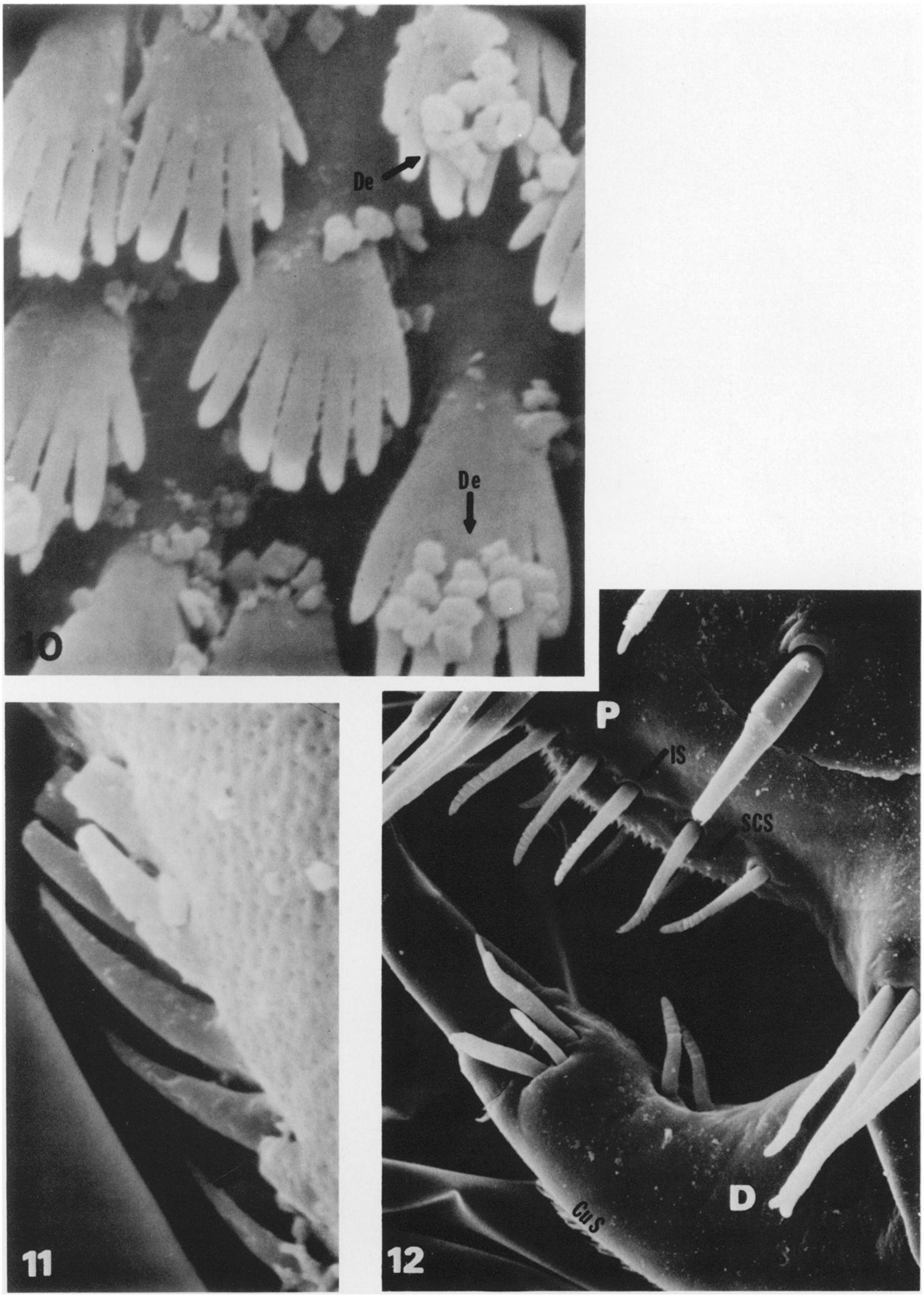
Orchestia, new species, female.—Gnathopod 1, as in *Talitroides,* is unmodified (Fig. 1a), with only smooth setae. Gnathopod 2 also resembles those of the terrestrial species, with propodal, carpal, and meral processes covered with echinate fields (Fig. 1b). However, the individual scales are radiate, as in the male *Or-*



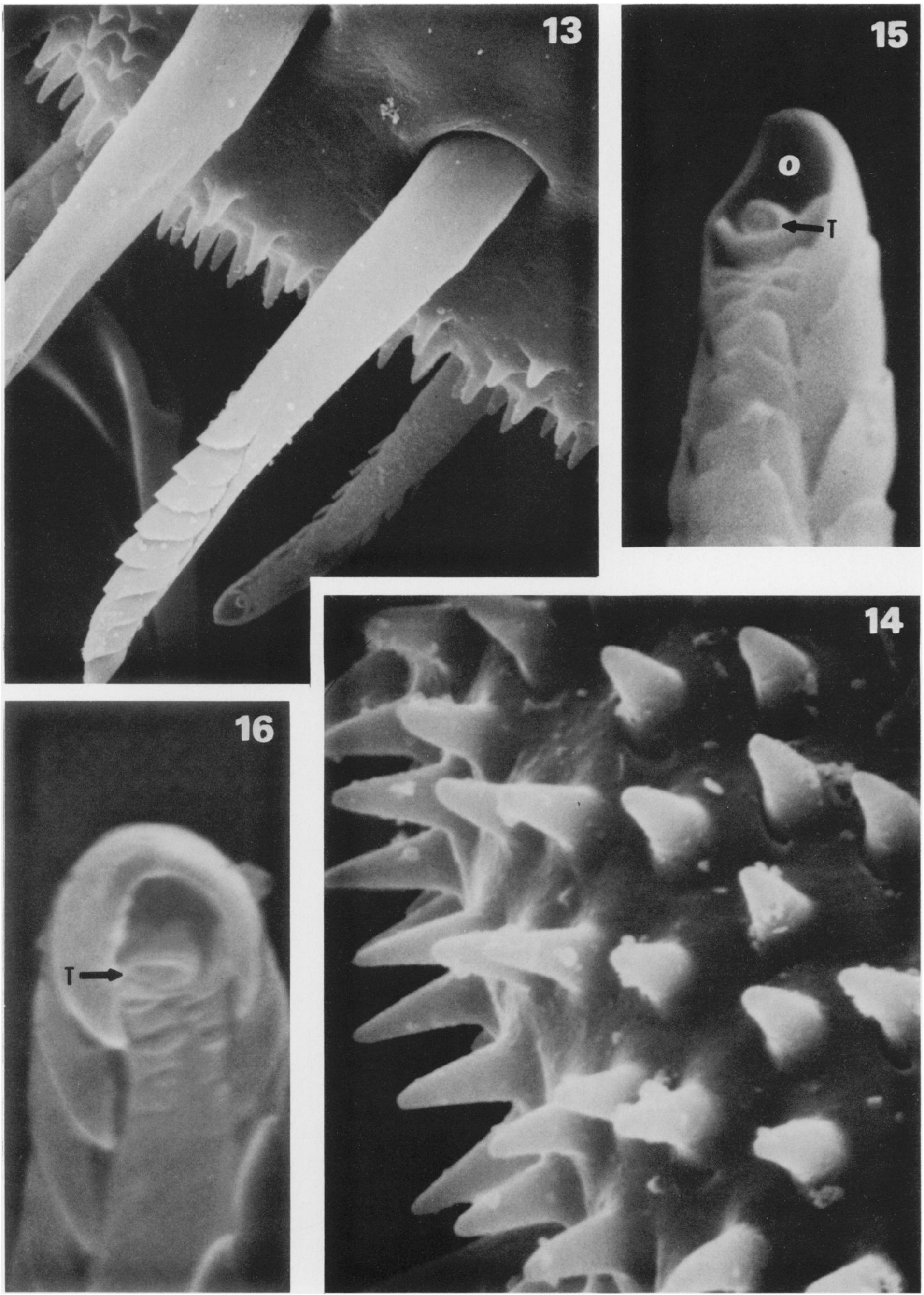
Figs. 2–5. 2, Gnathopod 1 of *T. alluaudi*, showing smooth (ss) and bifid setae (bs). D, dactyl; P, propod; C, carpus; and M, merus. ×300. 3, Gnathopod 2 of *T. alluaudi*. Echinate fields are apparent on propod (P) and carpus (C). D, dactyl; IS, imbricated setae; ISS, imbricated serrate setae. ×300. 4, Enlargement of echinate field of bristle scales from gnathopod 2 of *T. alluaudi*. ×1,800. 5, Imbricated serrate seta of *T. alluaudi*. S, shaft; Sh, sheath; O, overhanging shield. ×9,700.



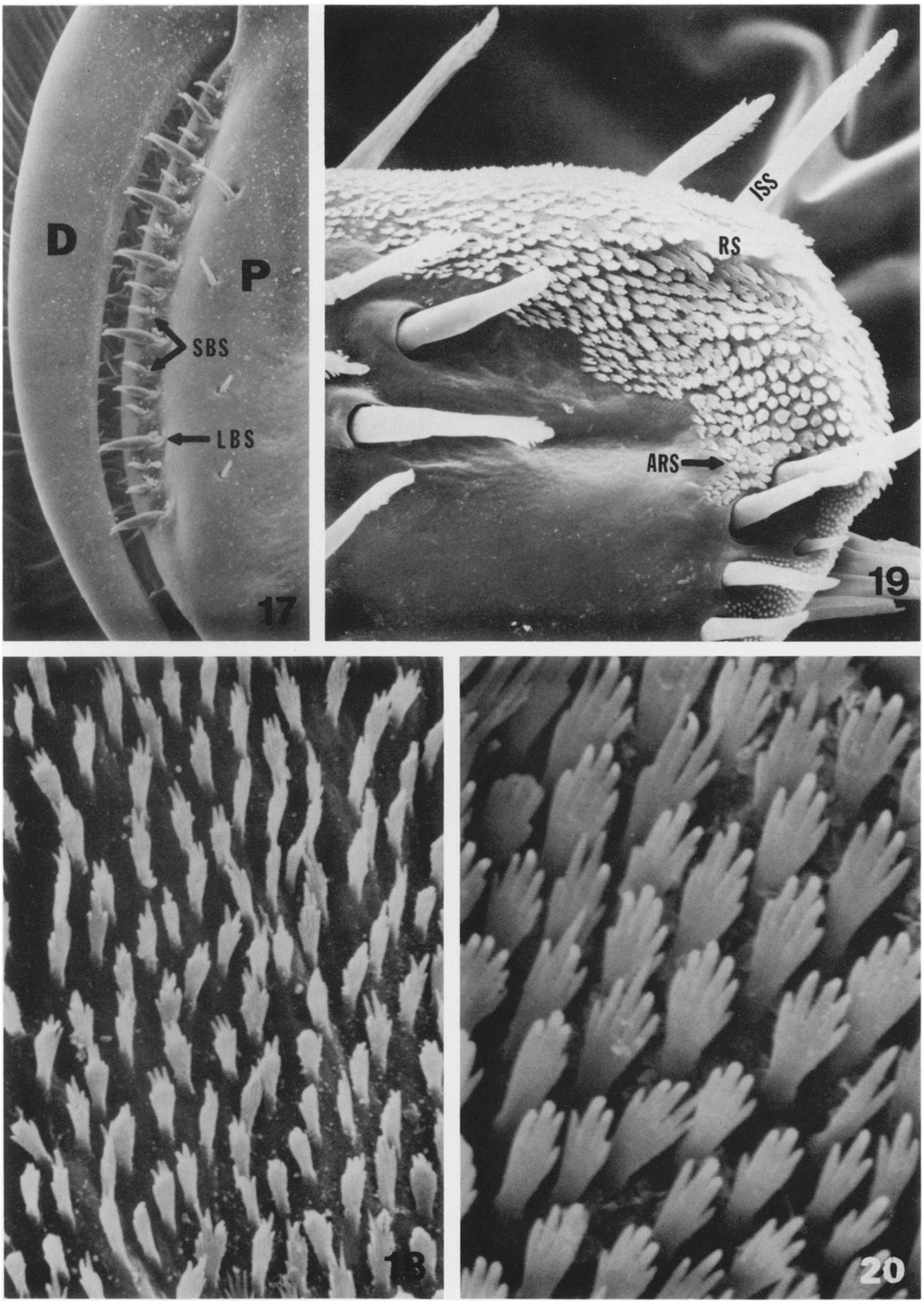
Figs. 6–9. 6, Bristle scales of *T. topitotum* gnathopod 2. Note hooked tips and detrital deposits. ×5,500. 7, Carpal echinate process of male *Orchestia,* new species, gnathopod 1. Arrows indicate path of receptor appendages. ×500. 8, Propodal echinate process of male *Orchestia,* new species, gnathopod 1. ISS, imbricated serrate setae. ×700. 9, Enlargement of radiate scales from male *Orchestia,* new species, gnathopod 1. Note smaller scales in upper left and detrital deposits. ×3,900.



Figs. 10–12. 10, Enlargement of radiate scales from male *Orchestia*, new species, gnathopod 1, showing detritus (De). ×16,000. 11, Curved spines on dactyl of male *Orchestia*, new species, gnathopod 1. ×10,000. 12, Dactyl (D) and propodal (P) palm of male *Orchestia*, new species, gnathopod 1. SCS, subacute conical spines on medial palmar ridge; IS, imbricated setae; and CuS, curved spines. ×700.



Figs. 13–16. 13, Enlargement of palm of male *Orchestia*, new species, gnathopod 1, showing imbricated setae arching over palm, openings directed medially. ×10,000. 14, Enlargement of subacute conical spines from male *Orchestia*, new species, gnathopod 1. ×10,000. 15, Imbricated seta from male *Orchestia*, new species, gnathopod 1. O, overhanging shield; T, terminal pore. ×20,000. 16, A second imbricated seta from male *Orchestia*, new species, gnathopod 1, showing terminal pore (T) to better advantage. ×28,000.



Figs. 17–20. 17, Propod (P) and dactyl (D) of male *Orchestia,* new species, gnathopod 2. SBS, small bifid setae; LBS, large bifid setae. ×200. 18, Radiate scales on propodal echinate process of female *Orchestia,* new species, gnathopod 2. Note sparse arrangement of scales. ×3,000. 19, Propodal process of male *O. grillus* gnathopod 1, demonstrating abraded (ARS) and normal (RS) radiate scales. ISS, imbricated serrate setae. ×1,000. 20, Enlargement of propodal process of male *O. grillus* gnathopod 1, showing radiate scales, ×5,000.

chestia, new species, instead of bristlelike, as in the terrestrial species. The scales are somewhat more sparsely arranged than in the males (Fig. 18).

A few imbricated serrate setae border the propodal echinate field. Imbricated setae are present near the palmar surface. In addition, subacute conical spines line the propodal palmar surface. A series of acute spines projects from the dactyl, facing the propod.

Orchestia grillus, male.—The first gnathopods of the male of this species also possesses propodal and carpal processes bearing echinate fields (Figs. 1c, 19). The individual radiate scales are somewhat more attenuated (Fig. 20) than those of *Orchestia,* new species (Fig. 10) and have 2–6 component spinules, as compared to 3–8 in the congener. Some scales appear to have been abraded (Figs. 19, 21). On the palmar surface of gnathopod 1, subacute conical scales are present, as in *Orchestia,* new species. About 20 imbricated serrate setae border the propodal echinate field (Fig. 19). Imbricated setae are also present, although in smaller number (10–15).

The second gnathopod of the male is very similar to that of *Orchestia,* new species. *O. grillus* possesses a double row of bifid setae; however, there are fewer of the smaller setae than are found on its congener. The surface of the medial palmar ridge is nodulate (Fig. 22), and the corresponding surface of the dactyl is imbricate (Fig. 23).

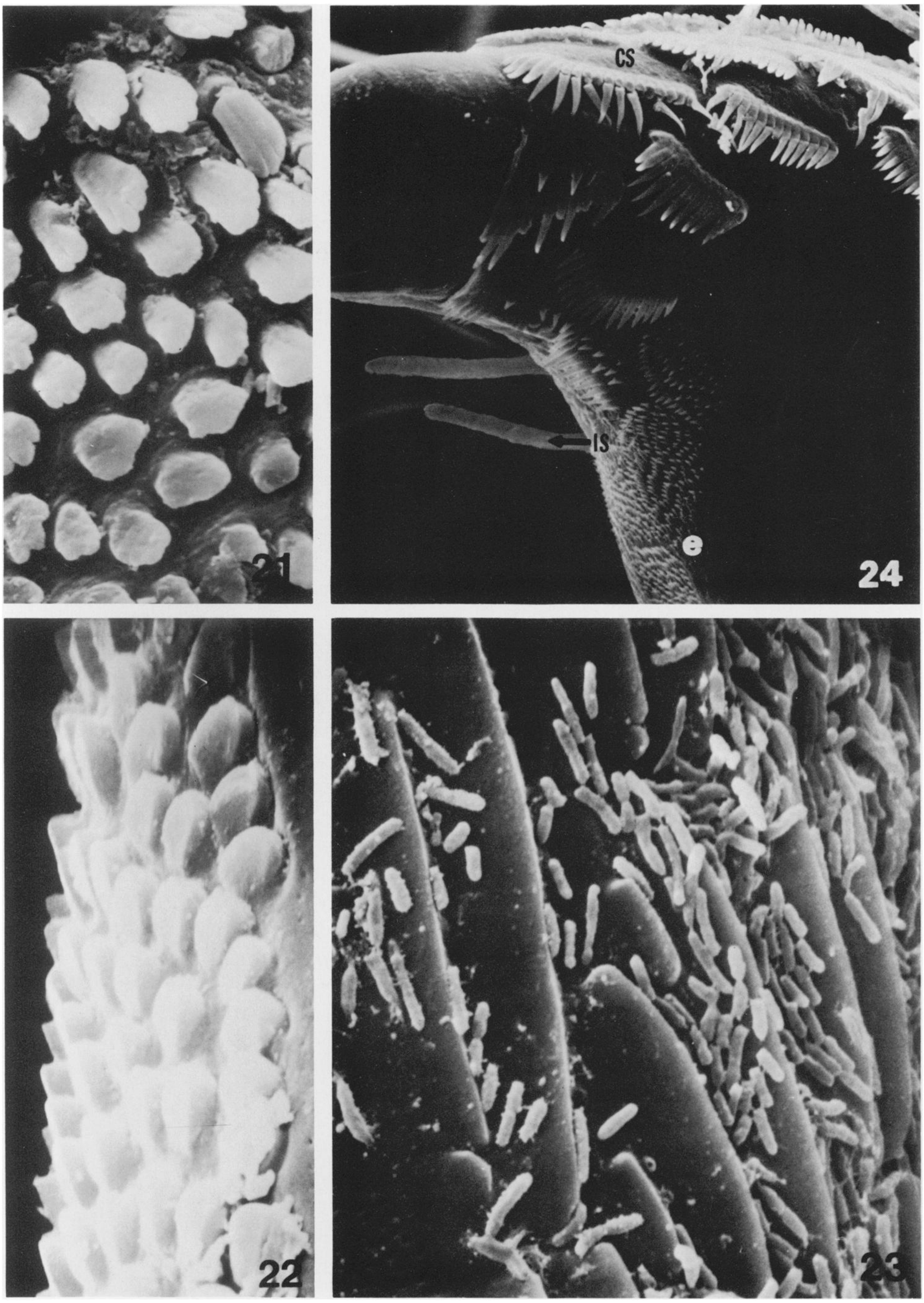
Orchestia grillus, female.—Gnathopod 1 is unmodified (Fig. 1a), with only smooth setae, as in female *Orchestia,* new species. Gnathopod 2 is like that of *Orchestia,* new species, except that *O. grillus* lacks the propodal subacute conical spines and the dactylar acute spines.

Hyalella azteca, male.—Gnathopod 1 is highly modified. The dactyl is armed with about 15 comblike scales (Fig. 24), located dorsally and directed medially. There are patches of echinulations (small prickles) located on the inner surface of the dactyl (Fig. 24). Many comb scales are also located dorsally and ventrally (Figs. 25, 26) on the propod, the former directed anteromedially and the latter directed ventrally. The palmar surface is armed with subacute conical spines (Fig. 27). Also, imbricated setae, located on both the dactyl and propod, arch over the palmar surface (Figs. 27, 28). These setae are longer than the imbricated setae described for the previous species (~85 μm vs. ~40 μm), and the rounded ridges appear to be more irregular.

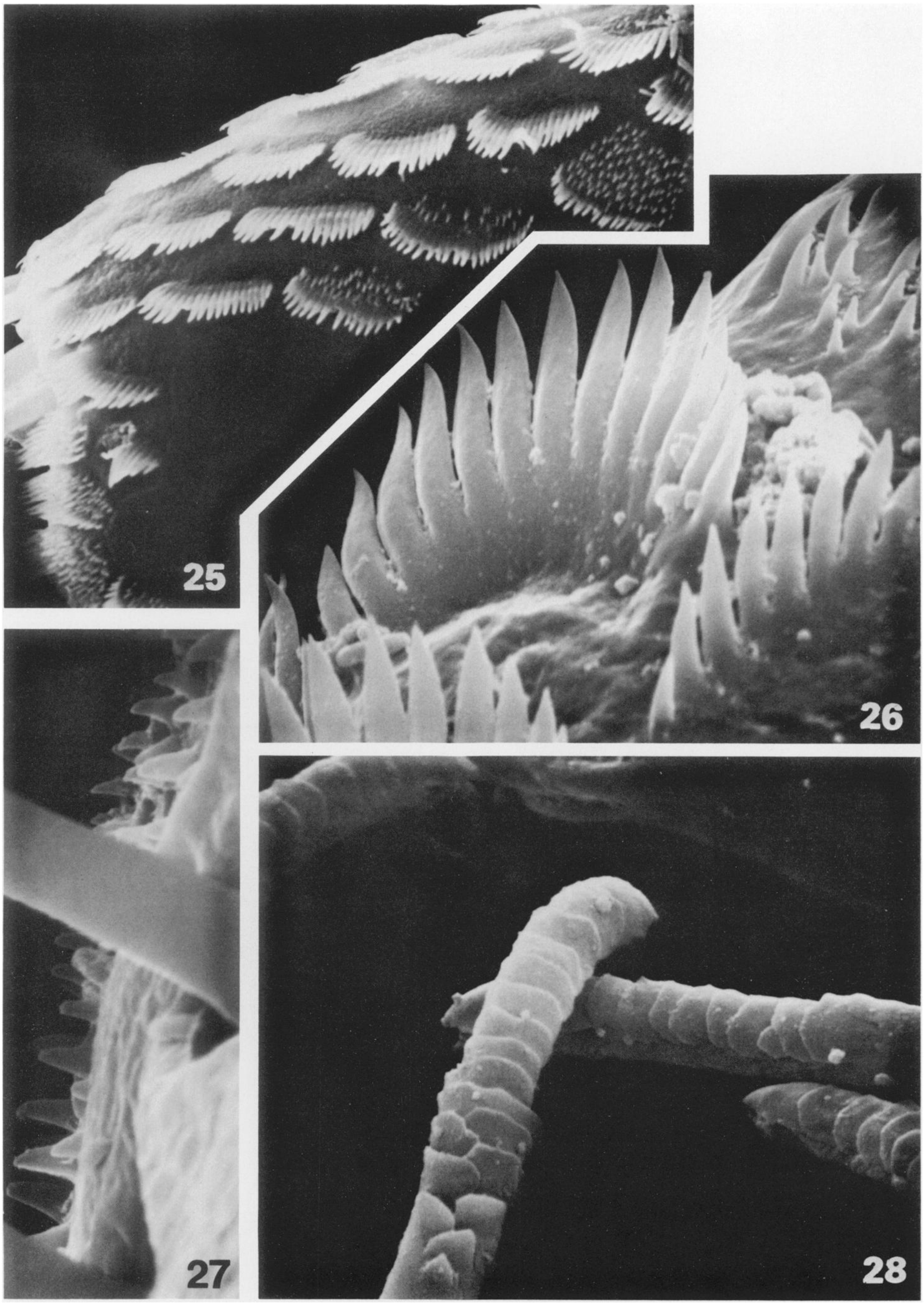
The carpus has an interesting distal concavity (Fig. 29). Dorsally there are about 15 patches of flattened comb scales (Figs. 29, 31). Ventral to the comb scales is a series of about 15 serrate setae (Fig. 29) which are longer than the imbricated serrate setae (~80 μm vs. ~40 μm). The individual serrations of the sheath are more filiform than those of the imbricated serrate setae (Fig. 5) and a terminal pore is present. The shafts of these setae have only a few, poorly defined imbrications near the tip (Fig. 30). These structures will be referred to as glabrate (almost smooth) serrate setae.

Located next to the setae (Fig. 29) is a series of structures resembling bisected cones. The outer side is rounded with projecting echinulations (Fig. 32), while the inner side is flattened and nodulate, as in Fig. 37. Finally, along the ventral margin of the concavity there are about 20 comb scales, often with echinulations at the base of each (Figs. 32, 33). The ventral margin of the merus is also armed with about 25 comb scales (Fig. 34) directed anteroventrally and closely associated with echinulations identical to those found on the carpus.

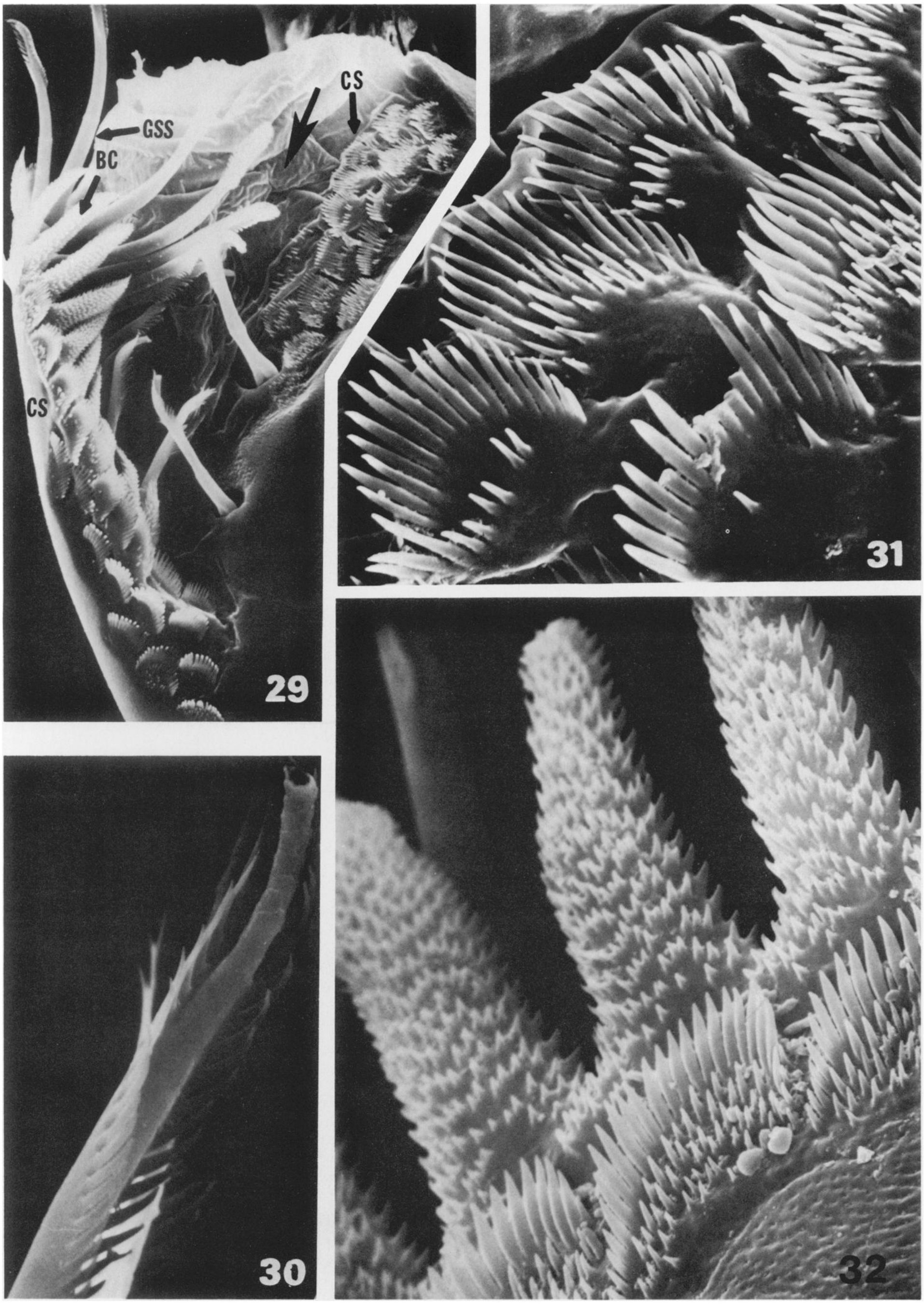
The male gnathopod 2 is powerfully subchelate. There is the typical double



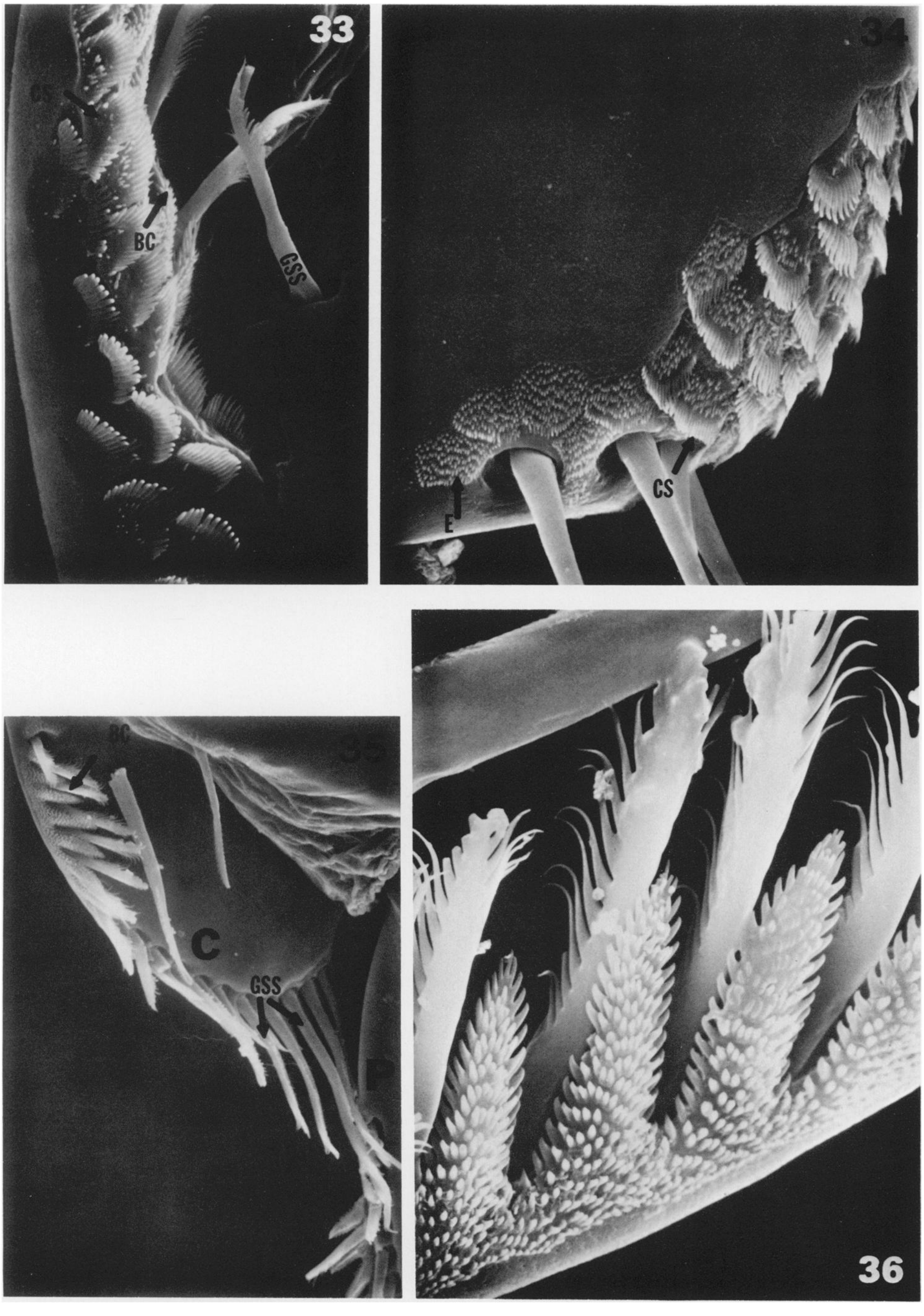
Figs. 21–24. 21, Enlargement of propodal process of male *O. grillus* gnathopod 1, showing abraded radiate scales. ×5,000. 22, Nodulations on medial palmar ridge of male *O. grillus* gnathopod 2. ×8,000. 23, Imbrications, facing medial palmar ridge, on dactyl of male *O. grillus* gnathopod 2. ×7,500. 24, Dactyl of male *H. azteca* gnathopod 1. CS, comb scales; e, echinulations; IS, imbricated setae. ×2,200.



Figs. 25–28. 25, Propod of male *H. azteca* gnathopod 1, showing comb scales located dorsally and distally. ×1,600. 26, Propod of male *H. azteca* gnathopod 1, demonstrating ventral comb scales. ×9,800. 27, Palmar surface of male *H. azteca* gnathopod 1, with subacute conical spines and bases of imbricated setae. ×9,600. 28, Imbricated setae, originating from the dactyl and propod of male *H. azteca* gnathopod 1. ×9,800.



Figs. 29–32. 29, Carpal grooming concavity of male *H. azteca* gnathopod 1. CS, comb scales; GSS, glabrate serrate setae; BC, bisected cones. Right is dorsal. Arrow indicates path of appendage. ×800. 30, Glabrate serrate seta from carpal grooming concavity of male *H. azteca* gnathopod 1, showing faint imbrications (I), near tip. ×4,500. 31, Flattened comb scales from carpal grooming concavity of male *H. azteca* gnathopod 1. ×5,000. 32, Enlargement of carpal concavity of male *H. azteca* gnathopod 1, demonstrating rounded sides of bisected cones (BC), comb scales (SC), and echinulations (E). ×4,500.



Figs. 33–36. 33, Enlargement of ventral margin of carpal concavity of male *H. azteca* gnathopod 1, with comb scales (CS), bisected cones (BC), and glabrate serrate setae (GSS). Left is ventral. ×1,500. 34, Ventral margin of merus of male *H. azteca* gnathopod 1. CS, comb scales; E, echinulations. Right is ventral. ×1,500. 35, Ventral margins of propod and carpus of male *P. hawaiensis* gnathopod 1, showing glabrate serrate setae (GSS) and bisected cones (BC). Note proximity of carpal and propodal grooming components. ×900. 36, Enlargement of glabrate serrate setae and bisected cones from carpus of male *P. hawaiensis* gnathopod 1. ×2,600.

row of stout setae, with one or two smaller setae located between each pair of larger ones. Both the palmar and dactylar surfaces are imbricate.

Hyalella azteca, female.—Gnathopod 1 is similar in general shape to that of the male, although the propod is somewhat narrower. The various setae and scales are similar to the male gnathopod 1 in type, size, number, and location.

Gnathopod 2 is much more slender than that of the male and is only weakly subchelate. The female *H. azteca* gnathopod 2 is similar to the male and has structures similar to those found on gnathopod 1.

Parhyale hawaiensis, male.—The propodal palmar surface is studded with subacute conical spines and the facing dactylar surface is imbricate. The ventral margins of the propod and carpus are armed with a long row of bisected cone-shaped structures (Figs. 36, 37) described for *H. azteca.* Between each of these cones is a glabrate serrate seta (Figs. 35, 36). The propodal and carpal components of this organ are continuous.

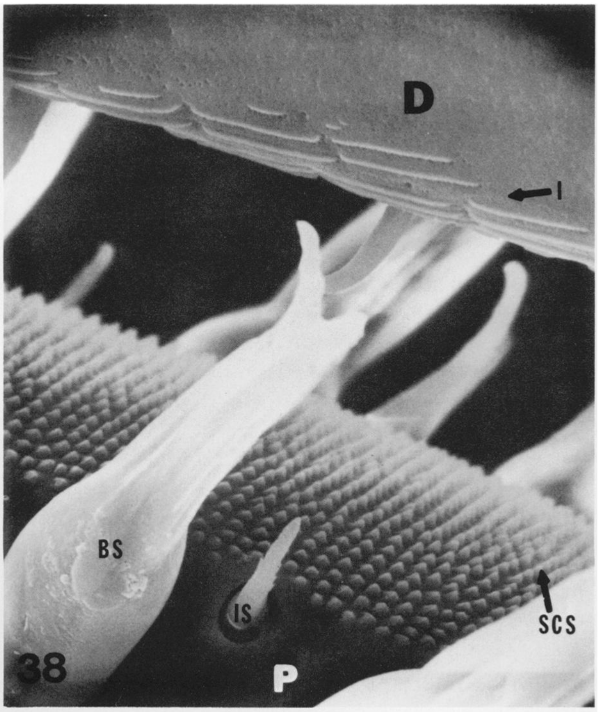
The propodal palmar surface of gnathopod 2 is armed with a great number of small subconical spines, arranged in irregular rows (Fig. 38). On either side of the palm are stout bifid setae and imbricated setae. The dactylar surface is imbricate.

Parhyale hawaiensis, female.—As in *H. azteca,* both the first and second gnathopods of the female are very similar to the first gnathopod of the male. Both of these female appendages exhibit the cone/glabrate serrate setae organ on the carpus and propod.

DISCUSSION

Some of the above-mentioned structures would clearly seem not to be of importance in grooming. Lowry (1974), in the description of a new member of the family Biancolinidae, related to the Talitroidea, discusses a series of subacute conical spines present on the palm of gnathopod 1 and striations on the opposing dactyl. He attributes a grasping function to these structures, and it appears that the subacute conical spines (Figs. 12, 13, 14, 27, 38) and corresponding imbrications (Figs. 23, 38) of *H. azteca* and *P. hawaiensis* and of *Orchestia* males serve the same purpose. The nodules of the male *Orchestia* second gnathopods (Fig. 22) are likely to function in a similar manner. These subacute conical spines, imbrications, and nodulations are located only along the palm and the facing dactylar surface (Fig. 38). These surfaces are brought into play while gripping substrate materials for support and locomotion (Holmquist, personal observation), while holding the female prior to copulation (Bousfield, 1973), and while grasping food materials during feeding (Smallwood, 1903; Holmquist, personal observation). The cuticular modifications should give more purchase during grasping. Schmalfuss (1978) has suggested that cuticular terraces of decapods also function to increase frictional resistance. However, during grooming bouts (Holmquist, 1981) amphipods are never observed to close the gnathopods on an appendage and pull the latter through the former. Since all grooming is performed without grasping, and the subacute conical spines, imbrications, and nodules are located only on the grasping surfaces, it is unlikely that these structures function in grooming.

Imbricated setae are seen on the gnathopods (Figs. 3, 12, 13, 24, 38) and the antennae (Fig. 39). Dahl (1973a, b) has described "chemosensory hairs" from talitrid amphipods that appear to be identical to the imbricated setae of *Talitroides* and *Orchestia* (Figs. 15, 16) and quite similar to the imbricated setae of *Hyalella*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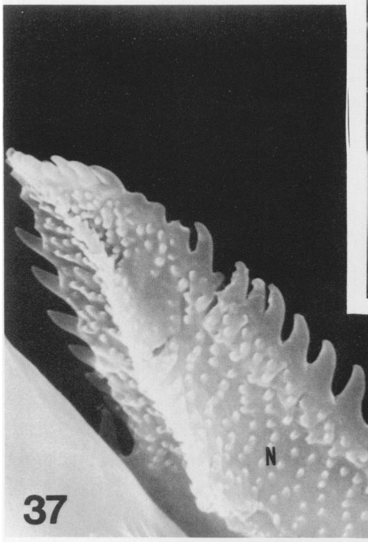
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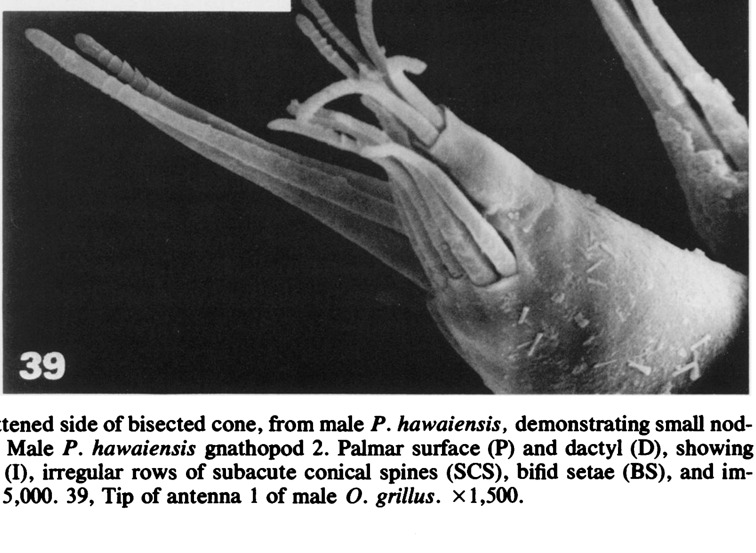
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Figs. 37–39. 37, Flattened side of bisected cone, from male *P. hawaiensis*, demonstrating small nodules (N). ×4,500. 38, Male *P. hawaiensis* gnathopod 2. Palmar surface (P) and dactyl (D), showing dactylar imbrications (I), irregular rows of subacute conical spines (SCS), bifid setae (BS), and imbricated setae (IS). ×5,000. 39, Tip of antenna 1 of male *O. grillus*. ×1,500.

(Fig. 28) and *Parhyale*. The term "seta" appears to designate better these structures than does the term "hair" (Thomas, 1970). The "simple setae" of Hindley and Alexander (1978) are also quite similar to talitroidean imbricated setae. Both Dahl (1973a, b) and Hindley and Alexander (1978) consider the imbricated setae to be chemosensory in nature. Interestingly, apical pores (Figs. 5, 15, 16, 30) of many chemoreceptors appear to be unnecessary for the penetration of molecules to the dentrites (Ghiradella *et al.,* 1968a, b; Ache and MacMillan, 1980).

As Factor (1978) has pointed out, there is some controversy with regard to the function of serrate setae. Shelton and Laverack (1970) and Farmer (1974) suggest that serrate setae of lobsters are primarily chemosensory structures, with the serrations increasing the surface area of the receptor. Roberts (1968) and Bauer (1975) state that the serrations of decapod serrate setae are adaptations for grooming. Bauer argues that if surface area is important in determining structure in chemosensory setae, then the villous "squat hairs" of lobsters would be more adaptive. He states further that, given chemical permeability of the cuticle, as concluded by Ghiradella *et al.* (1968a, b), the teeth would still have to communicate with the lumen of the setal shaft in order to accommodate nerve endings. However, the serrations of crayfish (Thomas, 1970) and of shrimp (Bauer, 1975) are solid. Yet the fact remains that the serrate setae of *Homarus* mouthparts respond to chemical stimuli (Shelton and Laverack, 1970).

Bauer (1975) has also suggested, along with Felgenhauer and Schram (1979), that serrate setae may function both in grooming and in chemoreception. This approach is particularly interesting with regard to the glabrate serrate setae (Fig. 30) of *H. azteca* and *P. hawaiensis*. Morphologically, these setae appear rather similar to talitrid setae with a presumed chemosensory function (Dahl, 1973a, b) and are located on the anteroventral portion of the gnathopodal carpus, where they might prove useful in food location and discrimination. However, this area of the anteroventral carpus (Figs. 29, 36) has been observed to be instrumental in grooming (Holmquist, 1981). Indeed, it would be quite adaptive for a single setal type to perform several functions.

The imbricated serrate setae of *Talitroides* and *Orchestia* appear to be identical to Dahl's (1973a, b) chemosensory setae, with the exception of the serrate sheath. These setae border the fields observed to effect grooming (Holmquist, 1981) but are not intimately associated with these echinate areas. Electrophysiological work would be helpful in clarifying the functional status of both the glabrate and imbricated serrate setae.

The remainder of the described structures appear to be modifications for grooming, and such a functional assumption is supported by recorded grooming behavior. The behavioral observations which follow are taken from Holmquist (1981).

In the terrestrial *Talitroides* gnathopod 1 is relatively unmodified for grooming, and, in turn, it participates in proportionately fewer grooming movements than in any other genus (40% in *T. alluaudi* and 43% in *T. topitotum*). The first gnathopods do appear important in "coarse" grooming, as these appendages have been observed to scrape large wet clumps of sand grains, etc., from the appendages and body surfaces. Almost all gnathopod 1 movements are also performed by gnathopod 2, the latter demonstrating a larger (60% and 57% of total grooming) and more diverse repertoire. It was noted that gnathopod 2 arches into a sickle-shape when grooming. In this arched position, the echinate processes on the propod, carpus, and merus meet to form a continuous grooming organ. Figure 1b depicts gnathopod 2 in an almost arched position. Hindley and Alexander (1978) report the carpus-propod joint of *Penaeus* also being flexed during grooming, in order to bring two groups of cleaning setae into contact.

As previously noted, one of the major dangers to a terrestrial arthropod is abrasion of the cuticle by dust and spores and the resulting desiccation (B. D. Valentine, unpublished observation). This environmental pressure might be even more severe for recent terrestrial invaders, such as amphipods. The tiny bristle scales (Fig. 6), rather similar to the *filaments scutaires* described by Cals (1974) from an isopod, are aligned antagonistically to the path of receptor appendages. These pick up very small particulate matter (~0.2 μm in diameter). Thus, the second gnathopods (the major grooming effectors) of terrestrial amphipods may have become specialized for small particle removal, with gnathopod 1 used for coarse grooming. Male and female gnathopods are identical, as these species are neotenic.

Unlike *Talitroides,* the semiterrestrial *Orchestia* shows strong sexual dimorphism of the grooming appendages. According to B. D. Valentine (unpublished data on representatives of 59 orders and 141 families of arthropods), sexual dimorphism of arthropod grooming appendages is rare. However, relatively few arthropods, other than amphipods, have grooming effectors that also serve in copulatory behavior.

Male and female *Orchestia* possess one pair of gnathopods modified for grooming; however, modification is of gnathopod 2 in the female, and of gnathopod 1 in the male. Appendages are pulled through and across the echinate grooves and processes of the male gnathopod 1 (Figs. 7, 8). As in *Talitroides,* the scales are neatly aligned (Figs. 7, 8) so as to achieve the most purchase on the receptor appendage, probably facilitating detrital collection (Figs. 9, 10). The male *Orchestia* gnathopod 2, however, is of the large, primitive carrying type used to grasp the female's thoracic segments prior to copulation (Bousfield, 1973). Without much grooming modification, it is not surprising that the male gnathopod 2 shows no grooming modes in either *O. grillus* or *Orchestia,* new species. Thus, a mating specialization has evolved, despite its handicapping effect on grooming ability. This situation is similar to that of the male fiddler crab, whose large display cheliped cannot be used in food gathering.

Orchestia females possess gnathopods very similar to both sexes of *Talitroides,* although the processes of gnathopod 2 are armed with radiate, instead of bristle scales. As in *Talitroides,* these segments are arched into a sickle-shaped structure that is observed to fit receptor appendages and body surfaces quite well during grooming.

Like the semiterrestrial species, the aquatic species demonstrate marked sexual dimorphism. In the male, gnathopod 2 is of the large carrying type and does no grooming. Gnathopod 1 is modified for grooming, and the aquatic males perform all their grooming activities with this appendage. Gnathopod 1 of the marine *Parhyale hawaiensis* male possesses a comb of alternating glabrate serrate setae and bisected cones along the ventral margins of the carpus and propod (Fig. 35). Only this ventral margin makes progressive contact with receptor appendages during grooming bouts. Gnathopod 1 of the fresh-water *Hyalella azteca* male, however, has a diverse array of grooming structures, located on the dactylar, dorsal and ventral propodal, and ventral and medial carpal surfaces. In turn, all of these surfaces are brought into play in the behavioral repertoire. The carpal process is particularly important in grooming the pereopods and uropods.

The females of aquatic species perform grooming with both the first and second gnathopods, unlike the males. As expected, both first and second gnathopods possess specialized structures for grooming.

Both aquatic males and females possess the glabrate serrate seta/bisected cone combinations (Fig. 36). The setae and bisected cones are significantly larger than the small radiate, bristle and comb scales, and the curved spines. The presence of these larger combs could be an adaptation against the comparatively larger epizoites encountered in the aquatic habitat.

Ghiradella *et al.* (1968b) found that the arrangement of aesthetasc dendrites in the terrestrial hermit crab *Coenobita* little resembled that of its marine relative, *Pagurus,* but was rather similar to the arrangement in insects. The dendritic arrangement of *Pagurus* was much more like that of other marine but distantly related forms, e.g., *Cancer* and *Panulirus.* A similar situation is clearly present in the Talitroidea. Three groupings are apparent in Table 1. These groupings fall under the categories of terrestrial, semiterrestrial, and aquatic, and are mutually exclusive with regard to grooming structure. *Talitroides* and *Orchestia* (terrestrial and semiterrestrial, respectively), although they are related genera of the same family (Talitridae), are quite divergent. On the other hand, *Hyalella* and *Parhyale,* containing aquatic species, are in different families (Hyalellidae and Hyalidae, respectively) and yet are almost identical with regard to grooming structure. It is unlikely, therefore, that these groupings are an artifact based on phylogenetic relationship; rather, the better hypothesis is that this divergence is a result of adaptation to increasingly terrestrial habitats.

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LITERATURE CITED

Ache, B. W., and D. L. MacMillan. 1980. Neurobiology.—*In:* J. S. Cobb and B. F. Phillips (eds.), The Biology and Management of Lobsters 1: 165–213.

Albonyi, H. 1928. Über die Epizoen der *Orchestia cavimana* (Heller).—Arbeiten des Ungarischen Biologischen Forschungs-Institutes 2: 5–23.

Bauer, R. T. 1975. Grooming behavior and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae).—Zoological Journal of the Linnean Society 56: 45–71.

———. 1976. Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae).—Journal of Natural History 10: 415–440.

———. 1977. Antifouling adaptations of marine shrimp (Crustacea: Decapoda: Caridea): functional morphology and adaptive significance of antennular preening by the third maxillipeds.—Marine Biology 40: 261–276.

———. 1978. Antifouling adaptations of caridean shrimp: cleaning of the antennal flagellum and general body grooming.—Marine Biology 49: 69–82.

———. 1979a. Antifouling adaptations of marine shrimp (Decapoda: Caridea): gill cleaning mechanisms and grooming of brooded embryos.—Zoological Journal of the Linnean Society 65: 281–303.

———. 1979b. Sex attraction and recognition in the caridean shrimp *Heptacarpus paludicola* Holmes (Decapoda: Hippolytidae).—Marine Behaviour and Physiology 6: 157–174.

———. 1981. Grooming behavior and morphology in the decapod Crustacea.—Journal of Crustacean Biology 1: 153–173.

Bousfield, E. L. 1973. Shallow-water gammaridean Amphipoda of New England.—Cornell University Press, Ithaca, New York.

Cals, P. 1974. Mise en évidence, par le microscope électronique à balayage, de champs morphogénétiques polarisés, exprimés par les cellules épidermiques normales dans l' appendice locomoteur des Arthropodes; *Tylos latreilli* (Audouin) (Crustacé, Isopode) et *Periplaneta americana* (L.) (Insecte, Dictyoptère).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences Série D 179: 663–666.

Canaris, A. G. 1962. A new genus and species of mite (Lalaptidae) from *Orchestoidea californiana* (Gammaridae).—Journal of Parasitology 48: 467–469.

Carlisle, D. B. 1962. Some uncritical observations on the reproductive behavior in crabs and prawns.—Animal Behaviour 10: 383.

Dahl, E. 1973a. Antennal sensory hairs in talitrid amphipods (Crustacea).—Acta Zoologica 54: 161–171.

———. 1973b. Presumed chemosensory hairs in talitrid amphipods (Crustacea).—Entomologica Scandinavica 4: 171–180.

Factor, J. R. 1978. Morphology of the mouthparts of larval lobsters, *Homarus americanus* (Decapoda: Nephropidae), with special emphasis on their setae.—Biological Bulletin 154: 383–408.

Farmer, A. S. 1974. The functional morphology of the mouthparts and pereiopods of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae).—Journal of Natural History 8: 121–142.

Felgenhauer, B. E. 1979. A note on the scanning electron microscopy and hosts of the widespread peritrich ciliate *Lagenophrys labiata*.—Transactions of the American Microscopical Society 98: 591–595.

———, and F. R. Schram. 1978. Differential epibiont fouling in relation to grooming in *Palaemonetes kadiakensis*.—Fieldiana (Zoology) 72: 83–100.

———, and ———. 1979. The functional morphology of the grooming appendages of *Palaemonetes kadiakensis* Rathbun, 1902.—Fieldiana (Zoology) 73: 1–17.

Fenchel, T. 1965. On the ciliate fauna associated with the marine species of the amphipod genus *Gammarus* J. Fabricius.—Ophelia 2: 281–303.

Ghiradella, H. T., J. F. Case, and J. Cronshaw. 1968a. Fine structure of the aesthetasc hairs of *Coenobita clypeatus* Edwards.—Journal of Morphology 124: 361–386.

———, ———, and ———. 1968b. Structure of aesthetascs in selected marine and terrestrial decapods: chemoreceptor morphology and environment.—American Zoologist 8: 603–621.

———, J. Cronshaw, and J. F. Case. 1968. Fine strucutre of the aesthetasc hairs of *Pagurus hirsutiusculus* Dana.—Protoplasma 66: 1–20.

Heath, D. J. 1976. The distribution and orientation of epizoic barnacles on crabs.—Zoological Journal of the Linnean Society 59: 59–67.

Hindley, J. P. R., and C. G. Alexander. 1978. Structure and function of the chelate pereiopods of the banana prawn *Penaeus merguiensis*.—Marine Biology 48: 153–160.

Holmquist, J. G. 1981. The functional morphology of amphipod grooming appendages.—Master's thesis, Ohio State University, 75 pp.

Jakschik, H. D. 1967. Distribution of the ciliate fauna associated with the subterranean freshwater amphipod, *Bacturus mucronatus* (Forbes).—Master's thesis, University of Illinois.

Kitron, V. D. 1980. The pattern of infestation of the beachhopper amphipod *Orchestoidea corniculata*, by a parasitic mite.—Parasitology 81: 235–250.

Lowry, J. K. 1974. A new species of the amphipod *Biancolina* from the Sargasso Sea.—Transactions of the American Microscopical Society 93: 71–78.

Richie, L. E., and J. T. Høeg. 1981. The life history of *Lernaeodiscus porcellanae* (Cirripedia: Rhizocephala) and co-evolution with its porcellanid host.—Journal of Crustacean Biology 1: 334–347.

Roberts, M. H., Jr. 1968. Functional morphology of mouthparts of the hermit crabs, *Pagurus longicarpus* and *Pagurus pollicaris*.—Chesapeake Science 9: 9–20.

Schmalfuss, H. 1978. Structure, patterns, and function of cuticular terraces in recent and fossil arthropods.—Zoomorphologie 90: 19–40.

Scurlock, D. 1975. Infestation of the sandy beachhopper *Orchestoidea corniculata* by *Gammaridacarus brevisternalis* (Acari:Lalaptidae).—Bulletin of the Southern California Academy of Sciences 74: 5–9.

Shelton, R. G. J. 1974. Observations on the occurrence of an epizoic, blue-green alga on the chemoreceptor setae of the brown shrimp, *Crangon crangon* (L.).—Journal of the Marine Biological Association of the United Kingdom 54: 301–307.

———, and M. S. Laverack. 1970. Receptor hair structure and function in the lobster *Homarus gammarus* (L.).—Journal of Experimental Marine Biology and Ecology 4: 201–210.

Shomay, D. 1955. A contribution to the morphology, taxonomy, and bionomics of the epizoic peritrichous ciliate *Lagenophrys labiata* Stokes, 1887.—Ph.D. thesis, University of Illinois.

Smallwood, M. E. 1903. The beach flea: *Talorchestia longicornis*.—Cold Spring Harbor Monographs 1: 1–27.

Snow, P. J. 1973. The antennular activities of the hermit crab *Pagurus alaskensis* (Benedict).—Journal of Experimental Biology 58: 745–765.

Solon, M. H., and J. S. Cobb. 1980. Antennae-whipping behavior in the American lobster, *Homarus americanus* (Milne-Edwards).—Journal of Experimental Marine Biology and Ecology 48: 217–224.

Stokes, A. C. 1887. Notices of new American fresh-water Infusoria.—Journal of the Royal Microscopical Society 1887: 35–40.

Tararam, A. S., Y. Wakabara, and F. P. P. Leite. 1978. Notes on *Parhyale hawaiensis* (Dana), Crustacea-Amphipoda.—Bulletin of Marine Science 28: 782–786.

Thomas, W. J. 1970. The setae of *Austropotamobius pallipes* (Crustacea: Astacidae).—Journal of Zoology 160: 91–142.

Walker, G. 1974. The occurrence, distribution, and attachment of the pedunculate barnacle *Octolasmis mülleri* (Coker) on the gills of the blue crab *Callinectes sapidus* Rathbun.—Biological Bulletin 147: 678–689.

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ANNOUNCEMENT

At its meeting last October, the Board of Governors of the Society voted to institute an award for the Best Paper published in the journal each year. A committee chaired by Denton Belk (Our Lady of the Lake University of San Antonio) will select a paper from among those nominated by the members. The award will be presented for the Best Paper of Volume 1 of the Journal (1981) at the Louisville meeting in December.

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