

Feeding, Reproduction, and Sense Organs of the Hawaiian Anchialine Shrimp *Halocaridina rubra* (Atyidae)¹

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ABSTRACT: The Hawaiian endemic shrimp *Halocaridina rubra* Holthuis currently inhabits anchialine pools on Maui, Kaho'olawe, O'ahu, Moloka'i, and Hawai'i islands. Information is presented on the feeding, reproductive, and sensory biology of these shrimp. Feeding cheliped setae are of two types, serrated setae that scrape the substrate surface and filamentous setae that collect the loosened food materials or act as filters. The shrimp are primarily microphagous grazers that scrape the surface of the algal-cyanobacterial crust on pool substrates. This grazing activity is essential in maintaining the integrity of the crust, an actively growing matrix of plants, bacteria, diatoms, protozoans, and underlying siliceous and carbonate materials. Filter feeding is only observed in pools with dense phytoplankton blooms. The first and second pleopods of male and female shrimp are illustrated, and reproduction in captive populations from Hawai'i and O'ahu locations is described. Sense organs examined include the eye, aesthetasc hairs, campaniform sensilla, ringed setae, and abdominal pits with flared setae. The anchialine shrimp *H. rubra* appears to be a generalist, feeds as a microphagous grazer or filter feeder, is well adapted to the epigeal-hypogeal habitat in the pools, reproduces in the subterranean portion of the habitat, and is equipped with sensory structures that detect motion and chemical changes in the environment. Survival of this endemic species is dependent upon the continued integrity of its habitat, which is unique and sparsely represented on five of the eight high Hawaiian Islands.

THE ENDEMIC SHRIMP *Halocaridina rubra* Holthuis, 1963, or 'ōpae 'ula to the Hawaiians (Plate IA), has been found only in anchialine habitats on Hawai'i (Plate IB), Maui, Moloka'i, Kaho'olawe, and O'ahu (Maciolek 1983; unpublished manuscript on Kaho'olawe biological reconnaissance, 1992, The Nature Conservancy of Hawaii). Anchialine pools are brackish-water coastal features, occurring in recent lava flows on Hawai'i and Maui,

a bomb crater on Kaho'olawe, a lake on Moloka'i, and in limestone formations on O'ahu. All connect to the underlying water table and are influenced by tidal fluctuations (Holthuis 1973).

The crust composition and feeding appendages of the shrimp were examined to elucidate the feeding mechanism and food resources of *H. rubra* in the anchialine pools in North Kona, Hawai'i. This study preceded an exclusion experiment to compare the impact of *H. rubra* and introduced exotic fishes on the growth of crust components and any subsequent changes in the benthic biota, which will be reported in a later publication.

Observations of feeding behavior and an inventory of the gut contents of *H. rubra* from the anchialine system at Cape Kīna'u, Maui, have been described (Wong 1975). Based on those studies and observations by others (Courlet 1976, Maciolek 1983), it is apparent

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PLATE I. *A.* The Hawaiian anchialine pool shrimp *Halocaridina rubra* (photo by M. Lee). *B.* An anchialine pool surrounded by 'a'a lava near 'Anaeho'omalu, North Kona, Hawai'i. The orange cyanobacteria crust covers the rocks and is exposed at low tide.

that *H. rubra* is primarily a microphagous herbivore with chelipeds that remove food materials from the surface of the crust, and maxillae that transfer the loosened plant and cyanobacterial fragments to the mouth. Some diatoms and cyanobacteria from the guts of Maui shrimp were identified (Wong 1975). Laboratory and field studies have shown that *H. rubra* is also attracted to insects that float at the surface, carrion, and commercial fish food (Wong 1975, Maciolek 1983; J.H.B., pers. obs.).

Information about the reproduction of these shrimp is limited to populations maintained in the laboratory, because berried shrimp have not been found in the pools. Larval stages were described from a single brood of a specimen of *H. rubra* collected at Cape Kīna'u, Maui (Couret and Wong 1978). In this study we describe the structure of male and female reproductive appendages and report on reproduction in captive populations.

Anchialine Pool Environment

Holthuis (1973) defined anchialine pools as bodies of water without surface connections to the sea that have measurable salinities and undergo tidal fluctuations. Salinity of the pools varies from less than 2 ‰ to 33.5 ‰ or more, depending upon proximity to the ocean and groundwater sources that percolate through the lava from adjacent land and mountain slopes. The 'Ewa, O'ahu, pools are 4 ‰ and West Hawai'i (Kona coast) pools are usually 6–15 ‰, except for Lua o Palahemo at South Point, Hawai'i, where salinity is 20 ‰ at the surface and 34 ‰ at 20 m (Table 1). The pools have water chemistry profiles for nitrate, phosphate, and silicate that are typical of coastal groundwater (Brock et al. 1987). The shrimp live in relatively calm waters that may be disturbed at the surface by wind, and the entire pool water mass is affected by tidal exchange through the floor of the pool and probably by lateral flow between adjacent pools. In this anchialine pool habitat these shrimp occupy two physically different habitats, the epigeal or well-lighted shallow pools and the hypogeal habitat of dark crevices in the water table below the pools.

TABLE 1
LOCATION OF SHRIMP OR CRUST SAMPLING SITES ON
HAWAI'I AND O'AHU

ISLAND	SITE
Hawai'i, South Kohala	Waikoloa: Waikoloa Anchialine Pond Preserve
North Kona	Kūki'o
South Point	Lua o Palahemo: near the shoreline at Ka Lae
O'ahu, Southwest O'ahu	Puhi Ula: Ka'u District 'Ewa: adjacent to the beach park
Northeast O'ahu	Kahuku: aquafarm well water

The typical benthic assemblage that covers the bottom of many shrimp-inhabited pools is composed of cyanobacteria, associated filamentous algae, and diatoms, forming an orange crust (Plate IB). This orange crust of anchialine pool substrates is a biosedimentary structure with an irregular, nodular surface bearing short filamentous epiphytes (Figure 3A) that give it a green or brown tinge (Plate IA). The upper surface is the actively growing part of the community. The cyanobacteria deposit lamina of crystalline pillars of aragonitic carbonate (Wong 1975), each layer representing a previous living surface like "algal stromatolites" or "algal mats" (Golubic 1973). Monaxon crystals that do not have any specific orientation are visible with light microscopy on the growing surface. Shrimp feed by "brushing" this crust with the cheliped setae of the first two pairs of pereopods.

The shrimp are typically bright red and can be so abundant that the pond water and sediment surface appear red. They frequently co-occur with the red alpheid shrimp *Metabetaeus lohena* Banner & Banner, 1960, which is much less abundant than *H. rubra*, and also less frequently with rare species of procaridid, hippolytid, and palaemonid shrimps (Holthuis 1973, Maciolek and Brock 1974, Maciolek 1986).

MATERIALS AND METHODS

Specimens of *H. rubra* and small pieces of crust were collected from the Waikoloa

Anchialine Pond Preservation area (WAPPA; Brock et al. 1987) in South Kohala on West Hawai'i (Table 1) and preserved in phosphate-buffered 2% glutaraldehyde or 2% formaldehyde in December 1990. Some material was prepared for scanning electron microscopy (SEM), and a portion of the formalin-fixed specimens was retained for light microscopy. Specimens for SEM were stained with 4% osmium tetroxide, dehydrated to absolute ethanol, critical point dried, and transferred to metal stubs with adhesive tabs. Specimens were coated with gold-palladium and examined with an SEM (Hitachi S-800). Samples of crust and mineral deposits on lava rock were collected for elemental analysis. These specimens were air dried and pulverized for X-ray analysis or attached with adhesive tabs to metal stubs, desiccated, and carbon coated. They were viewed with an ISI SS 40 SEM with a Princeton Gamma-Tech probe for elemental analysis. Powder X-ray analysis was done on a Syntag PAD V. Morphological details were also seen by examining living and preserved specimens of *H. rubra* and exuviae of captive shrimp. Exuviae were collected from the aquaria, mounted on slides with glycerol, and viewed with a compound microscope. Because of their rarity, O'ahu shrimp were not sacrificed, but the few that died in aquaria were preserved and measured. Behavioral observations of shrimp were made in the field and laboratory, sometimes with the aid of a hand-held lens.

RESULTS

Cheliped Morphology and Feeding Biology

Atyids differ from typical shrimplike crustaceans in lacking pincer chelae on the first and second pereopods. The dactyl is blunt and apposable to the propodus; both dactyl and propodus bear thick tufts of long setae.

The cheliped setae of the first and second pereopods (Figure 1A) are arranged in tightly packed rows at the tips of the propodus and dactyl (Figure 1B). There are two basic kinds of setae, serrated and filamentous (Figures 1C, 2), and variations of both. Serrated setae (Figure 2*a,b*) are about one-third the length of the filamentous setae and are located in the innermost row. Filamentous setae (Figure 2*c-f*) are the longest and most numerous setae and compose the outer rows. Filamentous setae of fixed specimens appear to be slightly flattened, especially at the tips (Figure 1F), and have more filaments originating nearer the tips than toward the bases. A few short undifferentiated setae are present on the ends of the innermost row.

The serrated setae are broad and flat, with a heavily serrated margin on one side and a row of overlapping denticles along the other margin (Figures 1D,E; 2*a,b*). Each tooth or serration has three to four small teeth along the inner edge (Figure 1E). There are about 20 of these serrated setae on each dactyl and propodus. The setae roll up and overlap each other in preserved specimens (Figure 1D) and are extended in live shrimp by hemocoelic pressure. The serrated setae each have two rows of microsetae along their length (Figure 1D,E). Microsetae have recurved hooks at the tips and are present on both sides of many of the flat surfaces of the setae although some had broken off at the base (Figure 1E). Filamentous setae (Figures 1F; 2*c-f*) have tips with sparse flexible filaments along one margin and closely packed, short, stiff bristles resembling a comb along the other. At the base of the comb is a single, anteriorly directed barb (Figure 2*e,f*). These setae can be recognized easily in lateral view by the comb and barb along the one margin.

The serrated setae, which resemble the cutting edge of a saw blade, scrape the crust's surface, and the long filamentous setae collect and entangle the loosened bacteria and algae.

FIGURE 1. A. Anterior region of *Halocaridina rubra* with chelate first pereopods below the antennae. Scale = 300 μm . B. Chelae with tufts of long setae at the tips of the propodus and dactyls. Scale = 200 μm . C. Innerface of chela showing filamentous and serrate setae. Scale = 20 μm . D. Serrate setae have one margin with denticles, the other with a row of serrate teeth. Scale = 4.5 μm . E. High magnification showing toothed serrations, denticles, and microsetae. Scale = 2 μm . F. Tips of filamentous cheliped setae. Scale = 10 μm .

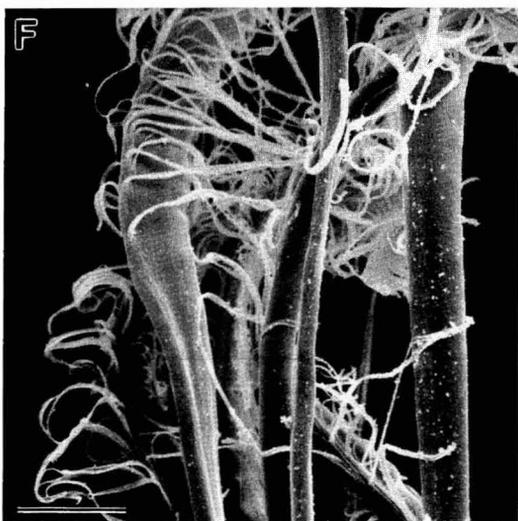
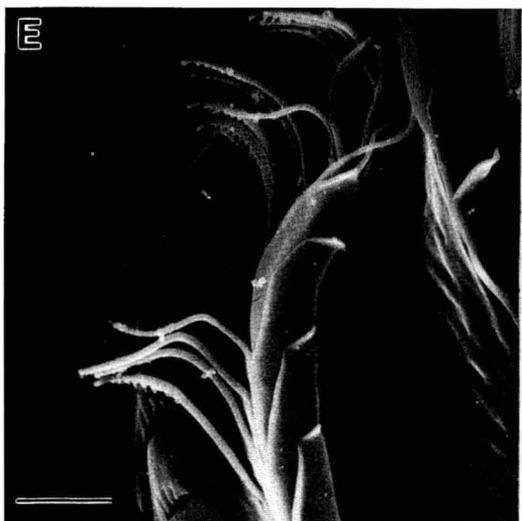
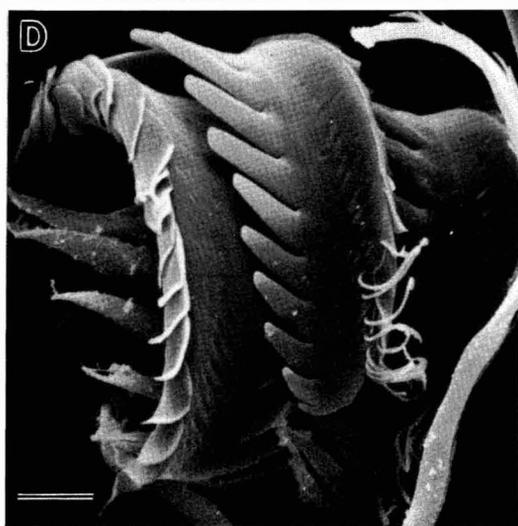
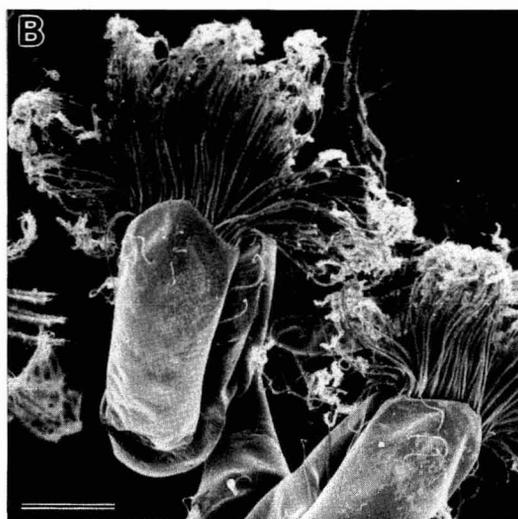
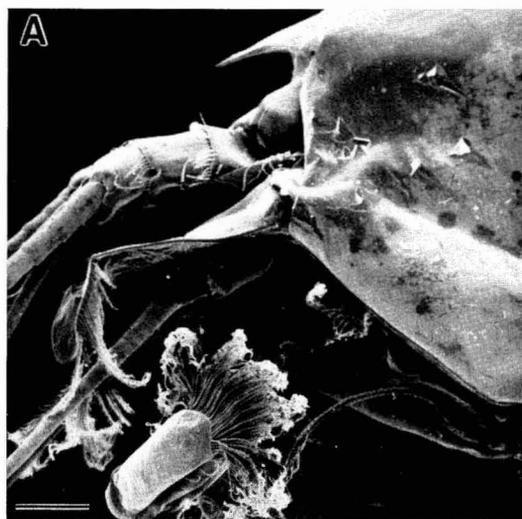




FIGURE 2. Variation in structure of cheliped setae. *a, b*. Serrate setae from inner face of cheliped tuft. *c*. Face view of filamentous seta. *d, e, f*. Lateral views of filamentous setae showing pectinate tips, barb at base of comb, and denticles along margin (*e*). All drawn using $\times 100$ objective and oil immersion.

The role of the microsetae (hooklike extensions of the serrated setae) is not clear, but their structure (Figure 1E) suggests that they may hold the serrate setae together as they scrape the substrate. When the cheliped setae are loaded with food particles, they are held beneath the head region and the food is transferred to the mouth by the first and second maxillipeds. After the food materials have been removed from the chelipeds, they may be groomed further by the third, fourth, and fifth pereopods or they resume brushing. Colonies of rod-shaped bacteria were present at the tips of the dactyl and propodus of some of the shrimp chelipeds prepared for SEM. These bacteria were oriented parallel to each other and formed dense patches near the bases of the setae.

These shrimp exhibit two feeding methods in the anchialine pool habitat. The first has

been described as plucking (Maciolek 1983), grasping (Wong 1975), scraping (Bailey-Brock et al. 1991), and brushing food from the substratum. In this method both pairs of chelipeds (pereopods 1 and 2) are sequentially applied in the open position, with the palm down, to the substrate and then lifted up and reapplied in rapid succession. The second mode has been described as filter feeding (Maciolek 1983) and filtration (Wong 1975). In this method both pairs of chelipeds are held so that the fans of setae are open and directed anteriorly. As the shrimp swims, the fans filter small particles from the water. This is considered to be the typical feeding mode of stream-dwelling atyids, but these shrimp remain stationary with the fans oriented into the current. The first method is most commonly observed when the shrimp are on a substrate; the second is seen only sometimes when the shrimp are in

phytoplankton-rich pools and they are swimming or otherwise off the bottom of the pool.

When the shrimp are feeding on the bottom of the pools, the brushing action of the chelipeds probably has a scraping or tearing effect on the filamentous algae and bacteria. We suggest that the crust surface is grazed by this activity and the length of the algal filaments is kept cut down, preventing the crust from being totally overgrown by epiphytes. This feeding method of *H. rubra* fits the definition of a grazer.

The shrimp are also known to feed in the water column while swimming slowly away from the bottom. This occurs when there are dense phytoplankton populations in the water. The cheliped fans are extended and filter the phytoplankton from the water (Maciolek 1983; R.E.B., pers. obs.). Presumably the slender tendril-like extensions at the tips of the numerous filamentous setae play an important role in filter feeding.

The shrimp show various kinds of locomotory activities, some of which may be associated with food searching; others are in response to disturbances. Locomotory activity includes swimming across the substrata, swimming up toward the pool surface and returning to the bottom (often with ventral surface uppermost), and walking. Swimming is facilitated by pleopod beating. In dense populations of shrimp this upward swimming behavior is seen in response to a disturbance, such as a piece of food dropped into the water, and it is contagious, so that shrimp that are nearby also swim up off the bottom. This behavior has been likened to popcorn kernels exploding in response to the increasing heat in the pan. When shrimp are food searching and checking the bottom, the chelipeds are opposed to the substratum, rubbed against each other, or held up under the head while walking on the remaining three pairs of pereopods. The pleopods usually provide the forward momentum, especially when walking is combined with short phases of activity moving one or two body lengths before resting or longer periods of darting swimming, moving five or six body lengths across the bottom. When swimming slowly, the shrimp moves off the bottom and then descends to a new posi-

tion at a relatively slow pace. This is repeated, making a series of low arching movements as the shrimp swims across the substratum.

The Benthic Food Resource

The benthic food resource is a mix of algae and bacteria (Wong 1975). Many of the algal cells consumed are diatoms, and the frustules are recognizable in the gut contents. Some of the bacteria are filamentous and photosynthetic and others are cocci and rods and some lack chlorophyll. The combined algal-bacterial complex forms an orange crust typical of many Kona coast and some Maui pools (Maciolek and Brock 1974, Maciolek 1986). Filamentous and branching chlorophytes overgrow the threadlike cyanobacteria (e.g., *Lyngbya*, *Schizothrix*, *Oscillatoria*, and *Scytonema* spp.), spirochaete (*Spirulina*), and coccid blue-greens (Figure 3A–D). Two species of folliculinids (ciliate protozoans) were found on the surface, both flask-shaped, one with a short neck and the other with an elongate neck (Figure 3C,D). Six species of diatoms were found with the SEM: two naviculoid species (*Cymbella* and *Nitzschia*), *Synedra* sp., *Melosira* sp., *Rhizosolenia* sp., and an Achnanthes, *Coconeis* sp. The naviculoids were the most abundant in the samples examined with the SEM. *Cymbella* sp. (Figure 4A–C) was often so dense it dominated the substrate (Figure 3C,D). *Nitzschia* sp. (Figure 4D) was also present, and individuals often adhered to each other, forming stellate colonies. A few angular sediment particles and amorphous material that may have formed around mucilage secreted by the diatoms and blue-greens were evident with the SEM.

Crust samples from two sites on the Kona coast (solid crust from Kūki'o and thinner structures from Waikoloa, Table 1) were first carbon coated and then analyzed for elemental composition. These specimens clearly showed that the dominant element is silicon, with smaller amounts of seven other elements. The Kūki'o crust had a ratio of silicon to magnesium to calcium of 7:1.2:1; in the thinner structures from Waikoloa, the ratio of the three most important constituents (silica, phosphorus, and magnesium) was 5.3:1.2:1.



FIGURE 3. A. Cyanobacteria crust from an anchialine pool. Filamentous algae were growing on the surface. Scale = 150 μm . B. Cyanobacteria filaments and coccids. Scale = 2 μm . C. Crust is a conglomerate of diatom frustules, cyanobacteria filaments, and folliculinid protozoans. Scale = 50 μm . D. Aperture of a folliculinid protozoan surrounded by naviculoid diatoms. Scale = 20 μm .

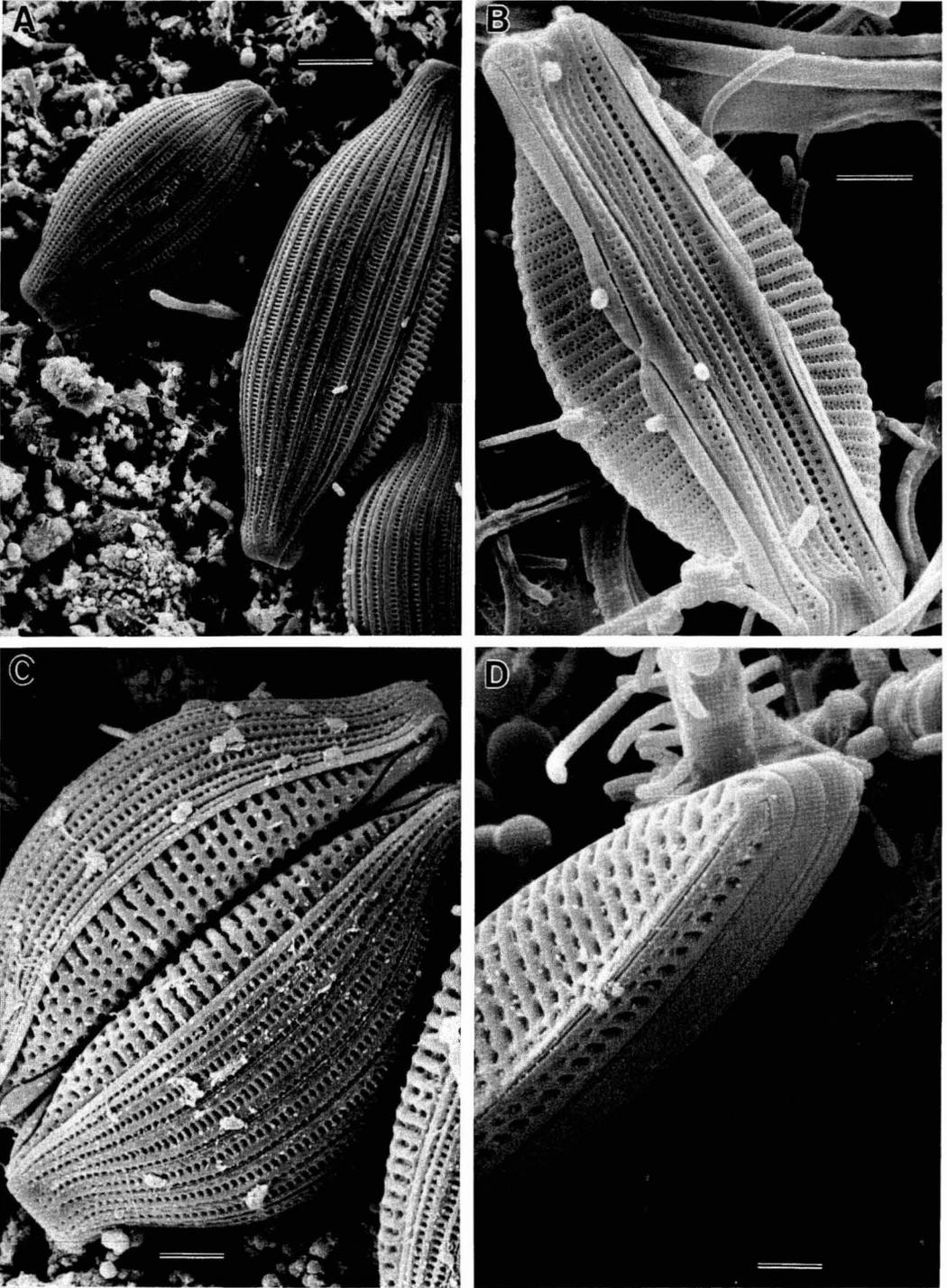


FIGURE 4. Diatoms of the cyanobacterial crust: A–C. Naviculaceae, *Cymbella* sp. A. Valve view. Scale = 5 μm . B. Raphe view. Scale = 2 μm . C. Pair of diatoms, valve view. Scale = 2 μm . D. *Nitzschia* sp. raphe and girdle view. Scale = 1 μm .

Powder X-ray diffraction showed that the Kūki'o substrate contained calcium in the form of aragonite and the Waikoloa sample lacked any crystalline material. The high silicon peak of the elemental analysis most likely represents an amorphous form that would not show up with the X-ray diffraction technique.

Sense Organs and Sensory Biology

Morphological details of sensory structures are described and compared whenever possible with similar structures in other crustaceans. We did not attempt to establish the neurological role of these structures for *H. rubra*.

EYES. The shrimp have a pair of dark, compound eyes borne on short, movable eyestalks (Figure 5A). They are located below the rostrum, which extends beyond the eyes, and above the antennal scales. They are shielded on either side by a blunt spine on the anterior margin of the carapace. The lensed portion of the eye is situated on the anterior-lateral aspect of the eyestalk and comprises about 50 ommatidia. In fixed specimens the lensed facets are round to octagonal and closely opposed to each other.

ANTENNULES AND ANTENNAE. Antennular bases originate below the eyes, and each has a pair of long, jointed flagella. Antennae comprise an antennal scale and a single long flagellum. Each flagellum bears short sensory hairs (Figure 5B) that occur singly or in pairs. Aesthetasc hairs (Figure 5C) are present on the proximal 10 joints of the outer antennule flagella (the exopods). They emerge at the anterior margin of a flagellar segment and at the center of a segment. The first two most distal segments lack aesthetascs, segments 3 and 4 have one row at the anterior margin, segments 5–10 have two rows, one at the middle and the other at the anterior margin of each, and segments 11 and 12 both have a single row at the anterior margin. Aesthetasc hairs have distal swollen regions with a pore or invagination at the tip of each, and jointed basal regions. They resemble the overall shape of *Ascellus* aesthetascs (Heimann 1984), but *H. rubra* aesthetascs have more elongate distal

regions and ringed or jointed bases. There may be a single hair, a pair, or one or two rows of three to six hairs on each of the 10 segments.

Membrane-covered pits thought to be campaniform sensilla (Figure 5B) were seen on the antennae and antennules, close to the origin of the sensory hairs. They may function as mechanoreceptors or chemoreceptors. If these are campaniform sensilla, they may be mechanosensitive, as described for lobster antenna sensilla (Derby 1982). Their smooth surface suggests that they are not the result of damage caused by specimen preparation.

ABDOMINAL PITS. Shallow pits containing clusters of slender, vase-shaped setae (Figure 6A–D) have been found on a number of abdominal segments. The pits are visible on exuviae at 40× magnification, but it required SEM examination to see the structure of the setae. The setae have flared tips that look as though they are open or only covered by a thin membrane. A membrane, however, is difficult to establish without using a labeled medium to see uptake by the setae. They are probably chemosensory but could have other functions because they are located on the abdominal region of the shrimp.

Pits contained a variable number of setae. Small groups of eight or 12 (Figure 6C) were found in pits on the lateroventral aspect of the telson and first abdominal segment; larger groups of 16, 20, 25, and 32 setae were found in dorsolateral pits of the telson (Figure 6A) and first, second, third, fourth, and fifth abdominal segments of some specimens. Setae of the dorsal pits of the first segment and telson (Figure 6A,B) were more slender, elongate, and numerous than those situated ventrally (Figure 6C,D). Within a pit the setae were in rows that were separated in the center by an open area with up to three pairs of pores (Figure 6A,B). The smallest clusters usually lacked the open area between the rows. The setae in *H. rubra* resemble those of *Gonodactylus* sp. (Stomatopoda), which are also open at the tips and arranged in rows in a groove (Laverack and Barrientos 1985), and which are thought to be chemosensitive.

RINGED MICROSETAE. These are small setae, 11–12 μm in length, that occur sparsely on the

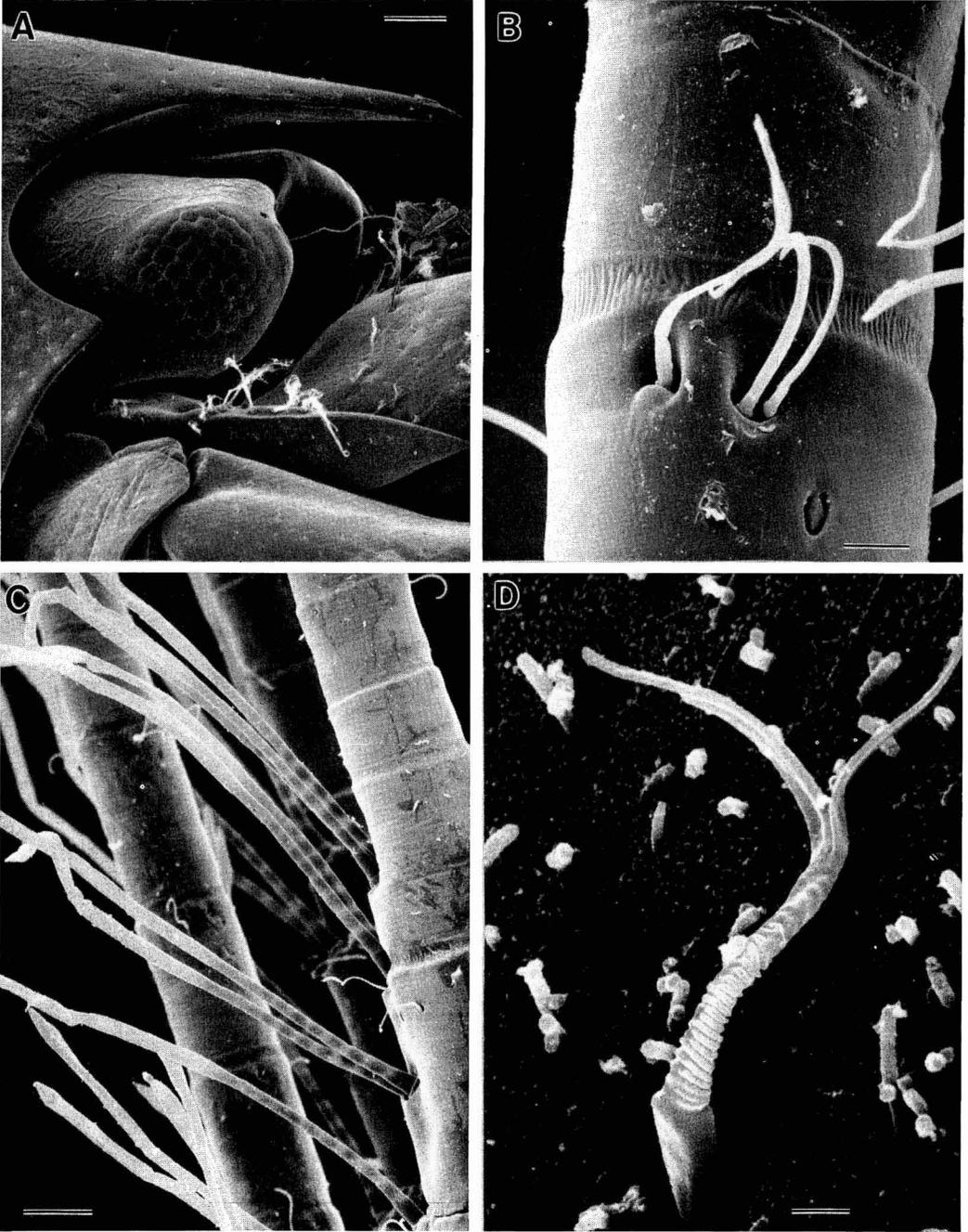


FIGURE 5. A. Compound eye of *Halocaridina rubra* below the rostrum and above the antennal scale. Ommatidia are evident as facets on the surface. Scale = 100 μm . B. Portion of an antenna with sensory setae and a campaniform sensilla. Scale = 5 μm . C. Bases of antennules with aesthetasc hairs. Scale = 30 μm . D. Microseta with base, ringed midregion, and four slender setules at tip. Scale = 1 μm .

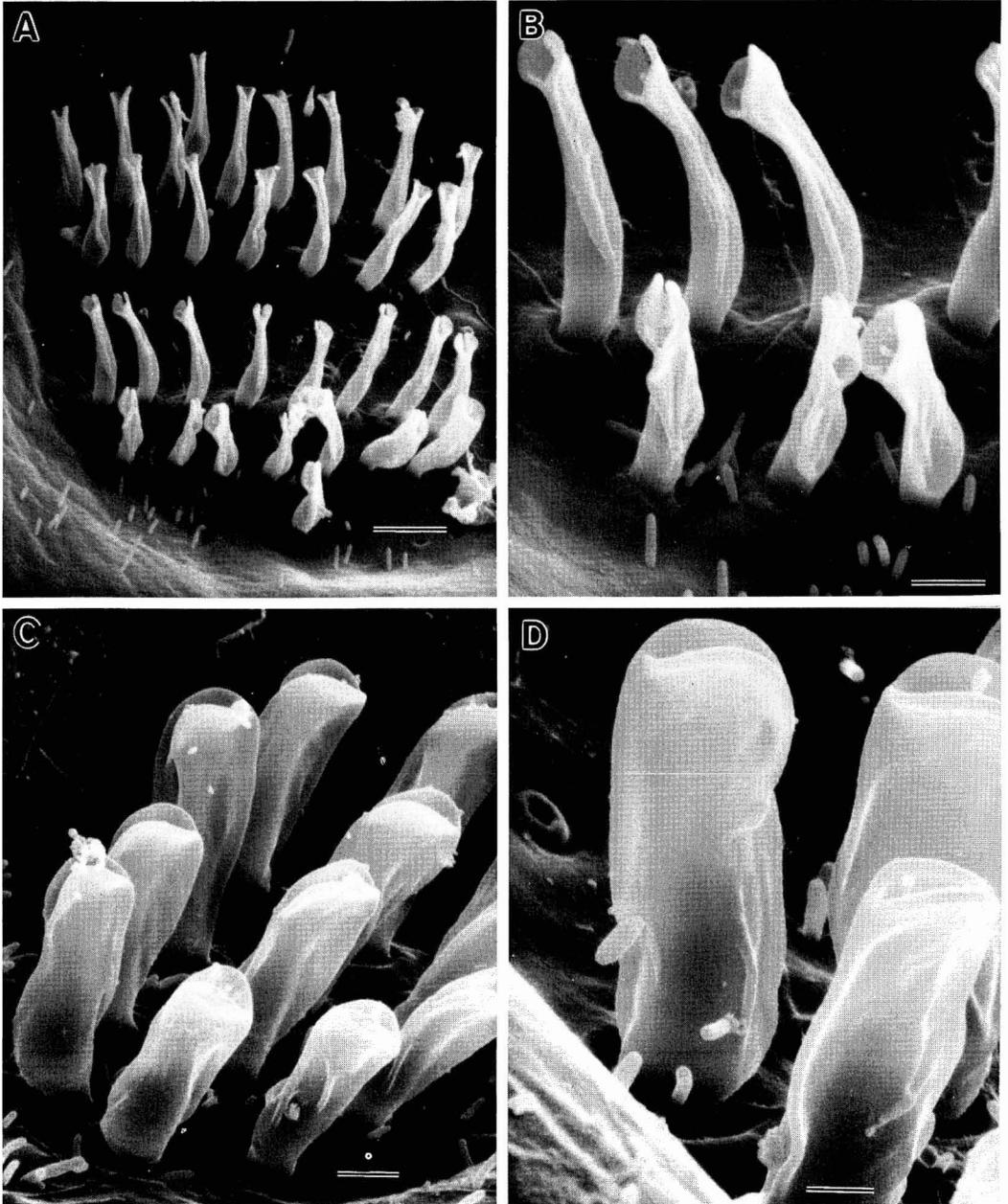


FIGURE 6. A. Abdominal pit on the dorsal aspect of the telson showing rows of setae and central open field. Rods are bacteria. Scale = 5 μm . B. Enlargement of setae in abdominal pit shown in A. Scale = 2 μm . C. Lower telson abdominal pit with three rows of setae. Scale = 2 μm . D. Enlargement of setae in abdominal pit shown in C. Scale = 1 μm .

carapace, abdomen, and antennal bases. Each seta emerges from a pit ca. 1 μm in diameter. It is composed of a basal region (Figure 5D) that is cylindrical but slightly flattened, a midregion of smaller diameter that is clearly ringed like a coiled hose, and a distal region that separates into four slender projections of similar length. These are the smallest structures observed on the external surface of *H. rubra*. The ringed microsetae resemble mysid setae (type B1), which have four slender setules at their tips and the coiled midregion (Crouau 1981) and possibly have some sensory function.

Reproductive Biology

In most caridean shrimp the structures on the first and second pleopod endopodites are the features used to distinguish mature males from females. These are difficult to see in specimens of *H. rubra* because of the small body size of these shrimp (does not exceed 14 mm in length). Portions of the first and second pleopods of a male paratype of *H. rubra* are illustrated in the species description (Holthuis 1963), but the equivalent female appendages are not shown. The first pleopods (Figure 7a–c) of both sexes have a short inner ramus and a longer outer ramus. The inner ramus of the male (Figure 7b,c) is elongate at the tip; that of the female (Figure 7a) has a more bulbous tip. The tip of the male inner ramus reveals eight short hooks (cincinuli); the female ramus bears setae on one margin but no cincinuli.

The second male pleopod (Figure 7e–g) has an inner ramus with two appendages, a flat, elongate lobe (the appendix masculina) and a slender appendix interna at its base (Figure 7e). The tip of the appendix interna has three cincinuli (Figure 7g). The second pleopod of the female (Figure 7d) has an inner ramus with one appendage, a slender appendix with three cincinuli at the tip. The most conspicuous distinguishing feature is the appendix masculina of the male's second pleopod. If this is lost or not visible on a permanent preparation, the slender shape of the inner ramus of the first pleopod also indicates a male (Figure 7b). These structures are visible

on exuviae, so sex can be determined in live specimens when they molt if kept in individual containers. Behavior indicative of mating was seen once in captive shrimp, but spermatophore transfer was not established (J.H.B.). Two shrimp were seen with ventrums and heads opposed on the floor of the aquarium. After separating, the lower shrimp righted itself and both shrimp swam away. This type of mating behavior has been described for *Penaeus vannamei* Boone and occurs in dark conditions (Yano et al. 1988). Mating of *H. rubra* most likely occurs in the dark; the single example described took place during the day under a rock. Spawning is assumed to occur in cryptic locations, such as beneath the rocks in aquaria or pools.

Shrimp populations kept in the laboratory since 1983 (from Honokōhau, Kona), 1986, 1992 (Waikoloa, Kona), and 1989 ('Ewa and Kahuku, O'ahu) have produced broods, although reproduction was not seen in our laboratory-held shrimp until food was added on a regular basis. After food is added, shrimp respond almost immediately by swimming up to the fish food floating on the surface, capturing a particle in the pereopods, and swimming down to the bottom. Shrimp with food are challenged by shrimp without, and within a short time excess food sinks to the bottom, where it is actively consumed. We first offered flakes when we observed shrimp on a cockroach carcass that had fallen into the tank. Before this, shrimp have been kept in aquaria for periods in excess of 3 yr without receiving any additional food. The shrimp feeding response appears to be to a chemosensory cue, but involvement of the entire population is stimulated by the increased activity in the aquarium. The Honokōhau population is the most prolific, and berried shrimp have been present throughout the year. The largest number of berried females was recorded in spring and early summer and the fewest in the fall. Females were observed carrying and dropping broods of 10–16 embryos. A brooding period of 38 days was noted by Couret and Wong (1978) for a single female held in a small aquarium. Larvae hatch as zoeae and swim toward the surface, showing a positive phototactic response. Zoeae maintain alternate up-

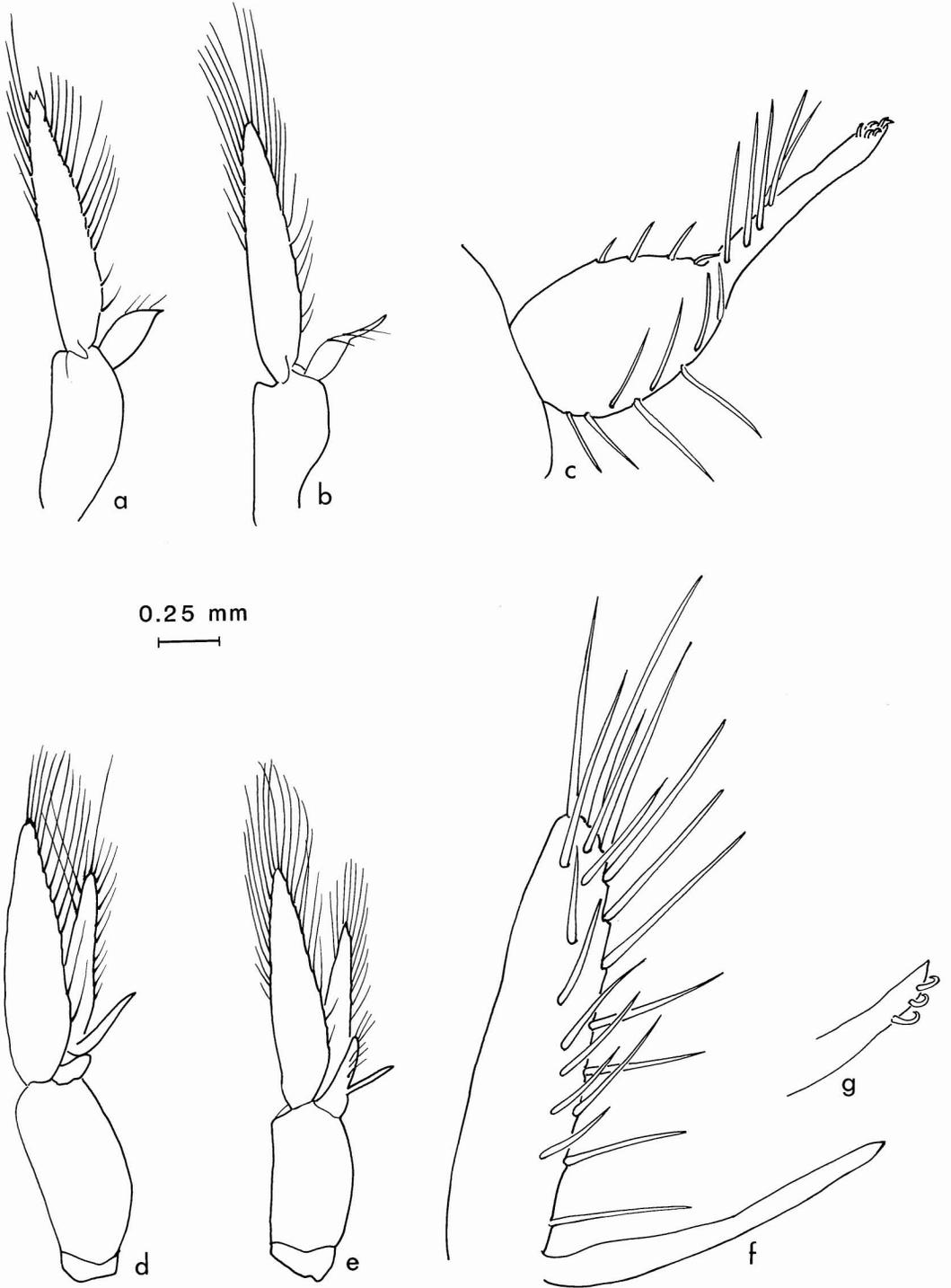


FIGURE 7. (*a, b, c*) First pleopods. (*d, e, f, g*) Second pleopods. *a*. Right first pleopod of a female. *b*. Right first pleopod of a male. *c*. Enlargement of an inner ramus of male shown in *b* ($\times 88$ oil). *d*. Right second pleopod of a female. *e*. Right second pleopod of a male. *f*. Enlargement of appendix masculina and appendix interna shown in *e*. *g*. Tip of appendix interna with three cincinuli ($\times 88$ oil). Scale for *a, b, d, e* = 0.25 mm.

ward swimming at the mean rate of 8.9 cm/sec ($n = 12$) and passive sinking, so move vertically and drift laterally in the water column. Zoeae may also hang almost motionless in a head-down position in the water. Megalopa, later-stage larvae, hang on the algal film growing on the sides of aquaria for brief periods and then continue upward swimming and sinking. The four zoea stages are transparent with brown thoracic regions and minimal red pigment that is not evident to the naked eye. Morphology of zoeae, megalopa, and juveniles is described in Couret and Wong (1978). Juveniles are readily distinguishable from the adults by their small size and pale coloration.

Morphological Variability

Specimens of *H. rubra* show variability in a number of morphological features, which

may represent genetic traits in the regional populations sampled (Table 2). Shrimp vary in the intensity of red coloration, size, curvature of the dorsal aspect of the carapace, rostrum length, number of long and short spines on the telson, and presence of one or two spines on the uropods (Figure 8a-c, Table 2).

The O'ahu shrimp from 'Ewa have least color, and shrimp from the Kona, Hawai'i, coast are the most intensely red (e.g., Wai-koloa and Kūki'o shrimp, even after 1 or 2 yr in captivity). When shrimp are disturbed, the chromatophores contract and they turn pale or lose the red color over a part or most of their body. This adjusts after variable periods of minutes or hours to the original intensity of redness. The 'Ewa shrimp and a population from Kahuku, O'ahu, are the smallest, whereas those from the Kona coast locations are the largest. Shrimp with slightly curved,

TABLE 2

MORPHOLOGICAL VARIATION IN 10 SHRIMP FROM EACH OF THREE HAWAI'I ISLAND LOCATIONS AND 'EWA, O'AHU ($n = 6$)

LOCATION	CARAPACE LENGTH (LEFT-RIGHT)	SEX (mm)	CARAPACE	ROSTRUM EXTENDS TO	UROPOD SPINES
Lua o Palahemo	2.5 (4)	F	Curved	End of eye	1,1
	3.0 (6)	F	Straight (1), curved (5)	End of eye	1,1
Puhi Ula	2.0 (1)	M	Straight	End of eye	1,1
	2.5 (4)	F	Straight (3)	Half first antennal segment (2)	1,1
	3.0 (3)	F	Slight curve (1)	End of first antennal segment (2)	1,1
			Straight (1), slight curve (1), curved (1)	End of first antennal segment (3)	1,1
	3.5	F	Slight curve	Base of first antennal segment	1,1
4.0	F	Slight curve	End of eye	1,1	
Kuki'o	2.5 (1)	F	Straight	Base of first antennal segment	2,1
	2.9 (1)	M	Straight	Base of second antennal segment	1,1
	3.1 (1)	F	Straight	Half first antennal segment	1,1
	3.5 (2)	M	Straight (1), curved (1)	Base of second antennal segment	1,1
	3.75 (2)	F	Straight (1)	Half first antennal segment	1,1
			Slight curve (1)	End of first antennal segment	1,1
	4.0 (3)	F	Slight curve (1), curved (2)	Base of second antennal segment	2,1
'Ewa, O'ahu	3.0 (5)	M (4)	Curved	Midway along eye	1,1 (2)
	3.25 (1)	? (2)	Curved	Midway along eye	1,1 (4)

NOTE: The number of shrimp with a given characteristic is shown in parentheses. Carapace length (mm) was measured from rostrum tip to posterior margin along the middorsum. Carapace curvature refers to the line along the middorsum as viewed from the side. Rostrum length is estimated according to extension of the rostrum tip over the eye and along the basal antennal segments as viewed from the side.

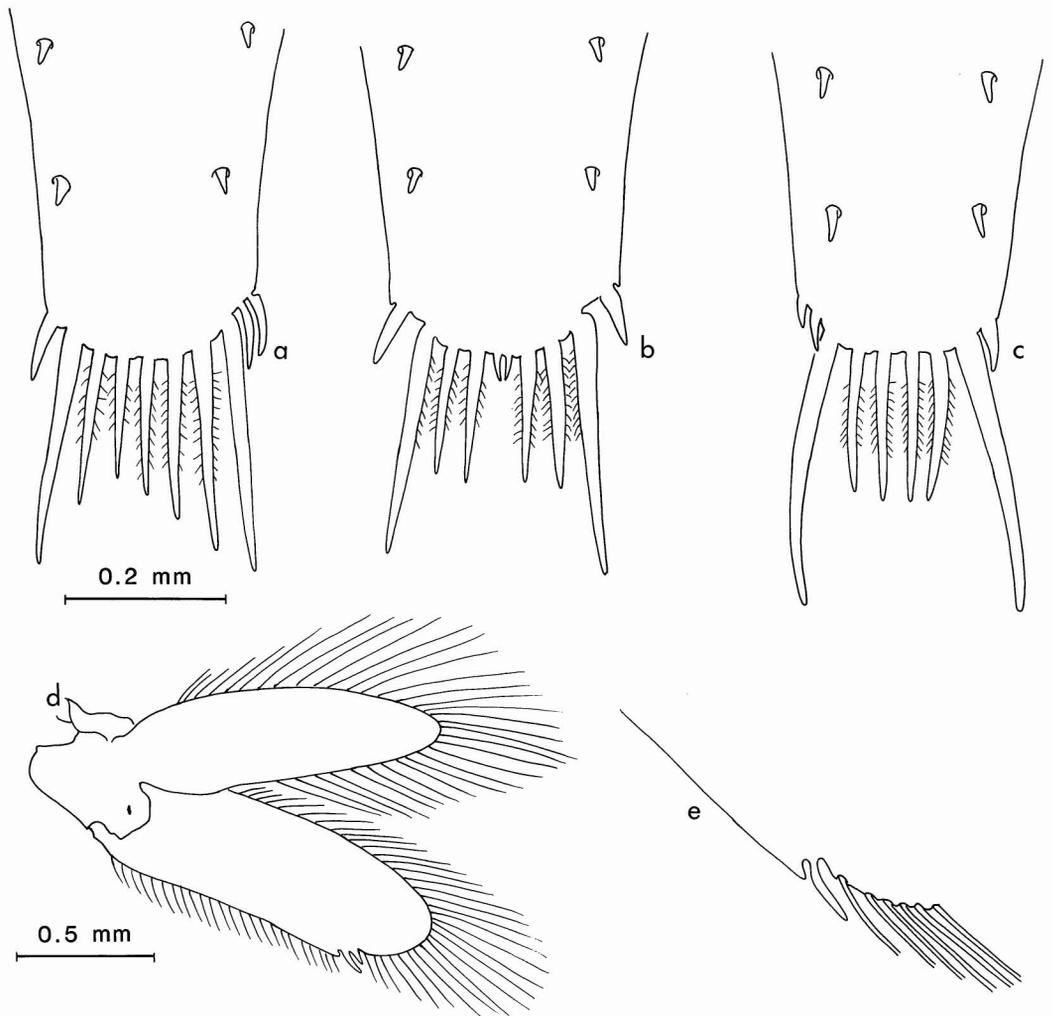


FIGURE 8. *a, b.* Telsons of *H. rubra* from Kūki'o, Hawai'i, showing dorsal, lateral, terminal, and in (*b*) median spines and spinules. *c.* Telson of shrimp from Puhi Ula, South Point, Hawai'i. *d.* Left uropod with two spines on the exopod. *e.* Right uropod with a single spine on the exopod of a shrimp from Puhi Ula.

curved, and straight carapaces are present in collections from Kūki'o, Puhi Ula (Ka'ū District), and Lua o Palahemo. The 'Ewa shrimp ($n = 6$) all had curved carapaces. There does not appear to be any correlation with sex, but none of the straight-back specimens exceeded 3.5 mm carapace length ($n = 11$). Rostrum length varies, extending over the eye, to the first antennular joint, midway along the second, or to the base of the second antennular joint. Only two Puhi Ula specimens had short

rostrums that were equal to the tip of the eye (Table 2), but all shrimp from Lua o Palahemo ($n = 10$) and 'Ewa ($n = 6$) had short rostrums.

There is considerable variation in the number of lateral and terminal spines (Table 2, Figure 8*a-c*) on the telson, and the short lateral spines may not be symmetrical on left and right sides (Figure 8*a,c*). There may be more than one lateral spinule on either side of the terminal spinules (Figure 8*a,c*), and the

number of terminal spinules varies. Holthuis (1963) said there are seven and illustrates a telson with six (fig. 1c in Holthuis [1963]), and possibly a very short median spinule is shown. In Figure 8, we show a telson with seven long spinules and an extra lateral spinule (Figure 8a) and two with six long spinules, one with a pair of short median spinules (Figure 8b), the other with an extra lateral spinule (Figure 8c). The outer pair of long spinules are consistently smooth; the inner ones bear fine setae. One fixed spine and one or two articulated spines on the diaeresis of each uropod is a diagnostic characteristic at the species level. We found differences between left and right sides: a female specimen from Ka'ū and two female shrimp from Kūki'o had two spines on the left uropod and one on the right (Table 2, Figure 8d,e). The description of *H. rubra* shows a left uropod with two spines (fig. 1c in Holthuis [1963]): the outer fixed spine and an inner spine. The congener *H. palahemo* Kensley & Williams, 1986, another red anchialine shrimp that is known to occur only in the Lua o Palahemo pool at South Point, Hawai'i, has one spine on the uropod. *Halocaridina palahemo* is distinguished from *H. rubra* by a number of other features, including length of the rostrum, curvature of the carapace, shape of chelipeds, and spination and length of pereopod joints (Kensley and Williams 1986). We see variability in some of these features among specimens of *H. rubra* from Kūki'o and the Ka'ū District (Table 2).

The variability in these morphological characters suggests that their use for diagnostic purposes may be questionable and that large sample sizes (ca. 100) should be examined to establish variation in external features of shrimp from populations in different locations. It would then be possible to establish if morphological variation between populations is sufficient for species separation (e.g., *H. palahemo* and *H. rubra*).

DISCUSSION

The salinity range of habitats occupied, variety of foods consumed, and morphological adaptations for food capture suggest that

H. rubra is well adapted to the many variable conditions that exist in the anchialine pools and subterranean habitat. This habitat is apparently more complex than that of freshwater streams, which are occupied by many other atyid species and are regarded as the typical atyid habitat (Fryer 1977). Life cycle characteristics such as few eggs per brood, advanced hatching stage, long-lived adults, and the inability to compete with visual predators also suggest that *H. rubra* are specialists in the anchialine pool habitat.

The functional morphology of feeding has been described for six species of freshwater atyid shrimp (Fryer 1977, Felgenhauer and Abele 1983). The cheliped fans of *Atya innocous* (Herbst) in Panama each comprise about 300 setae modified as scrapers, filters, and as chemoreceptors (Felgenhauer and Abele 1983). In fast-moving streams the setae are extended and the four open fans (two on either side of the head) oriented into the current capture suspended food. These shrimp may also scrape the substrate, as we describe for *H. rubra*. Another species found in similar habitats with fast-flowing streams, *A. margaritacea* A. Milne Edwards, competes with *A. innocous* for the fastest-flowing sections of streams and filter feeds in a similar manner (Felgenhauer and Abele 1983). The Hawaiian freshwater atyid *Atyoida bisulcata* Randall, 1840, occurs in fast-flowing lotic habitats on O'ahu, Hawai'i, and Maui and is predominantly a filter feeder although it also grazes the substrate ([as *Atya bisulcata*] Edmondson 1929, Couret 1976; [as *Ortmannia henshawi* (Rathbun, 1900)] Edmondson 1929, 1935). Other examples of grazing atyids are the Indo-West-Pacific *Antecaridina lauensis* (Edmondson, 1935) that occurs in the anchialine pools of Maui and Hawai'i Island and *Halocaridines trigonophthalma* (Fujino & Shokita, 1975) of the West Pacific; both have been described as pluckers (Maciolek 1983) and fit our definition of grazers.

Pool waters are generally clear and free of visible suspended sediment, so filter feeding in the water column occurs rarely. However, *H. rubra* has been observed filter feeding in pools on Maui (Wong 1975) and on the Kona coast. In a deep, phytoplankton-rich pool

(Lua o Palahemo, South Point, Hawai'i), *H. palahemo* (Kensley and Williams 1986) was seen (by a snorkeling observer) to swim and filter feed in the water column. Similar observations were made on Maui for *H. rubra* (Wong 1975). The South Point observation provides another example of filter feeding by atyid shrimp in these coastal pools.

Variation in morphology of rostrum, telson and uropod spination, and color are evident in the populations of *H. rubra* studied from Hawai'i and O'ahu. Some of these features are part of the species diagnosis of *H. rubra* and *H. palahemo*. Variation is seen within populations (e.g., telson and uropods, rostrum) and between islands (e.g., color). An electrophoretic analysis of the genetic composition of *H. rubra* populations from Hawai'i, Maui, and O'ahu, and of *H. palahemo* from Hawai'i indicates that these shrimp all belong to the same species; cladistic analysis of their phylogeny shows that Hawai'i shrimp are all similar, and that Maui and O'ahu shrimp show evolutionary relationships (M. A. Romano and L. S. Powers, unpublished manuscript on biochemical systematics of *H. rubra*, prepared for the U.S. Army Corps of Engineers, 1992).

The morphology of the cheliped fans of *H. rubra* resembles that of *Atyoida* (Chace 1983) and *Atya* spp., although chemoreceptor setae described for *A. innocous* (Felgenhauer and Abele 1983) are not evident on the Hawaiian shrimp (unless these are the short, undifferentiated setae of the cheliped mentioned earlier). Setae composing the cheliped fans enable the shrimp to either graze on the crust or filter feed. The crust represents a continuously renewing food source for *H. rubra*, in contrast to the situation of the stream atyids, which are more dependent upon water flow for filter feeding and to bring appropriate food materials to the habitat. It is in the hypogeal environment that *H. rubra* must reproduce and brood the developing embryos (Courret and Wong 1978, Maciolek 1983). These shrimp are very likely dependent upon the productivity of the pools for much of their food, and although bacteria and detritus may be eaten in the hypogeal portion of the habitat, this has not been demonstrated.

We suggest that *H. rubra* feeds in the epigeal portion of its habitat and reproduces in the hypogeal portion. The absence of berried females and larvae from the epigeal portion of the anchialine pool habitat (observations by a number of researchers over 23 yr) indicates that the conditions in the hypogeal environment may be more suitable for larval development than those in the epigeal region. These conditions may include waters of higher salinity and absence of visual predators. The upward swimming response of zoeae seen in the laboratory may be a behavioral adaptation by which larvae reach the vicinity of the lighted environment where metamorphosis occurs. Small juveniles are commonly observed on substrate in the pools.

Anchialine pools represent a unique ecosystem that is disappearing on the island of Hawai'i because of a number of anthropogenic perturbations. The development of large-scale resorts and access roads along the West Hawai'i coast has caused infilling of many pools. Resort development has made pools more accessible to the public, resulting in the introduction of exotic fish to serve as fish bait, and use as receptacles for trash. Anchialine pools containing exotic fish are devoid of shrimp because of predation, and the subsequent absence of shrimp appears to initiate changes in the benthic biology of pools. Filamentous algae grow over the substrate and cover the diverse bacterial/algal community that previously flourished in the pools. We contend that the shrimp are the keystone species in maintaining the benthic community of the anchialine pools.

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