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FEEDING BIOLOGY AND MOUTHPART MORPHOLOGY OF THREE SPECIES OF CORAL GALL CRABS (DECAPODA: CRYPTOCHIRIDAE)

Roy K. Kropp

ABSTRACT

This study refutes the long-standing hypothesis that coral gall crabs are filter feeders. *Hapalocarcinus marsupialis* collected mucus by fanning the third maxillipeds or by scratching the coral with the legs. *Utinomia dimorpha* used chelipeds to collect mucus and other debris, or to snip pieces of coral tissue. *Favicola rugosa* used mouthparts and chelipeds to make a mucous ball and sweep it along the coral surface to pick up mucus and debris. SEM photographs of the mouthparts of each species show setae ill suited for filter feeding, but useful for collecting coral mucus.

Coral gall crabs have been known for over 100 years, yet cryptochirid feeding biology is poorly known. Stimpson (1859) described *Hapalocarcinus marsupialis* as free-living, but feeding on coral polyps. Verrill (1867) considered the crabs parasitic on corals. Henderson (1906), finding live polyps in the gall, discounted Stimpson's idea that *Hapalocarcinus* fed on coral tissue. Potts (1915) presumed that gall crabs fed on nanoplankton drawn through the holes in the gall by the respiratory currents of the crabs. Potts' ideas have been cited frequently (Hiro, 1937; Marshall and Orr, 1960; Patton, 1967; Castro, 1976; Barnes, 1980; Mc-Laughlin, 1982).

There are indications that Potts' ideas are not valid. Patton (1976) briefly mentioned that *Hapalocarcinus* picks at coral tissue with its chelipeds and passes the material to its mouthparts. Reed *et al.* (1982) listed *Troglocarcinus corallicola* as an obligate coral mucus-feeder.

Here I clarify cryptochirid feeding biology by using anatomical studies to determine the food gathering apparatus available to the crabs, and behavioral studies to describe feeding activities. These studies showed that the crabs do not filter feed, but collect food from their host corals.

MATERIALS AND METHODS

Collection Data. – I collected crabs on their host corals at Apra Harbor, Luminao, and Agana Bay, Guam, during 1979–1981 and 1984. Crabs and corals were kept in the laboratory in large, flow-through sea-water tanks. I collected Hapalocarcinus marsupialis Stimpson, 1859, on Pocillopora damicornis and P. eydouxi; Utinomia dimorpha (Henderson, 1906) on P. eydouxi; and Favicola rugosa (Edmondson, 1933) on Leptoria phyrgia.

Feeding Behavior.—I used a dissection microscope to observe crabs feeding in their dwellings on small pieces of the host coral placed in a dish of sea water. Light from the microscope illuminator did not appear to affect crab behavior. It was necessary to remove the growing edge of galls of *Hapalocarcinus* to observe the crabs feeding, but not necessary to alter dwellings of the other crabs. Feeding was observed for at least 14 20-min periods per species. To test the results of feeding motions, I put a few drops of a carmine suspension in sea water onto the coral surface adjacent to the crab dwelling. Carmine rapidly coagulated into the mucous strings permitting observation of mucus movement patterns.

Scanning Electron Microscopy. – Crabs collected in 1984 were fixed in 3% glutaraldehyde and stored in 70% ethanol. I removed feeding appendages from these crabs and cleaned the appendages by brushing them with a fine brush. The gastric mill was removed from crabs, cut lengthwise along the ventral surface, and cleaned by gentle water currents created by passing a brush above the mill. Structures were dehydrated in a graded ethanol series, air dried, sputter coated with gold-palladium, and observed with a Cambridge S-100 or S-250 scanning electron microscope at accelerating voltages of 10–20 kv.



Fig. 1. a, Favicola rugosa, third maxilliped; b, F. rugosa, setae on inner lower margin of third maxilliped; c, Hapalocarcinus marsupialis, seta on palp of third maxilliped; d, Utinomia dimorpha, setae on palp of third maxilliped; e, U. dimorpha, setae on endopod of second maxilliped; f, U.

RESULTS

Crab Dwellings

Hapalocarcinus lives enclosed in a coral skeleton gall. Water circulates through the gall via small holes along the suture line between gall halves. The inside of the gall is lined with living coral tissue.

Utinomia lives in a pit in the coral skeleton. Surrounding the pit is a narrow border zone of dead coral in which brown, flocculent debris accumulates, and in which filamentous algae may occur. Coral verrucae next to the zone are eroded.

A narrow border zone of dead coral surrounds pits inhabited by *Favicola*. The host calyx wall completely surrounds the pit with the long axis of each septum perpendicular to the pit.

Feeding Behavior

Hapalocarcinus used chelipeds to grab coral tissue and pull it to the mouth, to pick mucous flocs off the coral, and to scoop material along the coral surface toward the buccal area. After such motions, the setae of the palp of the third maxillipeds wiped accumulated mucus from the chelipeds. Alternate or simultaneous fanning episodes of the third maxillipeds, usually less than 30-s long, drew carmine-marked mucus to the mouth. The legs assisted feeding by vigorously shaking in a plane perpendicular to the coral surface, thus actively scratching the dactylus on polyps and causing mucus to accumulate on the hooked setae of the dactylus. The chelipeds then picked the material off the dactylus and transferred it to the mouth. Usually only one leg shook at a time. Sometimes, after a shaking episode, the dactyli of two adjacent legs rubbed together casting accumulated material into the water near the crab. Fanning of the third maxillipeds pulled this debris to the mouth.

Utinomia used chelipeds to pick debris from its body or the wall of the pit and to grab debris from the border zone around the pit. Crabs snipped and ingested small pieces of tissue from the coenosteum fringing the border zone or from polyps. The chelipeds also probed the border zone or adjacent coral tissue, then flexed rapidly toward the mouth. Occasionally the claw squeezed coral tissue, then flexed toward the mouth. This scooping motion, followed by maxilliped fanning, moved mucous strings that had accumulated in the border zone to the mouth. Rarely, the chelipeds pulled mucus into a bolus that was eventually carried to the mouth and manipulated by the maxillipeds. This was similar to that described in detail for *Favicola*. Sometimes the third maxillipeds fanned independently of any cheliped action. The results of this fanning were unclear, but did not pull mucus to the mouth.

Favicola, other than one instance when a crab ingested a piece of coral tissue, used only one method to gather food. The chelipeds or maxillipeds pulled mucus into a bolus. One cheliped then clutched the bolus, swept it along the edge of the pit and back to the starting point, then transferred it to the other cheliped which repeated the action. After 2–31 repetitions of this criss-cross pattern, the bolus was taken to the mouth where it was rotated by the third maxillipeds while being vigorously probed by setae of the exopod of the second maxilliped. The crab grabbed the bolus with a claw and repeated the criss-cross pattern or expelled the

dimorpha, setae on endopod of first maxilliped; g, U. *dimorpha*, first maxilla (lower) and second maxilla (upper); h, F. *rugosa*, upper part of second maxilla. Scales: $a = 200 \ \mu m$; b, $h = 20 \ \mu m$; c, $d = 5 \ \mu m$; e, $f = 50 \ \mu m$; $g = 100 \ \mu m$.



bolus and formed a new one. Mucous strings, moved to the pit by coral ciliary action, were incorporated into the bolus being swept along the pit border by the criss-cross action of the claws.

Feeding Structures

Setal terminology is based on Kunze and Anderson (1979).

Maxillipeds. — The third maxillipeds (Fig. 1a) are similar in all three species. The inner margin of the ischium has few relatively short, simple setae along its entire length, and also has scattered serrate setae on its upper half (Fig. 1b). The palp of the third maxilliped has clumps of serrate setae on the carpus, dactylus, and along the inner margin of the propodus. Serrate setae may have distal setules forming a slight spoon (Fig. 1c), or setules terminating proximal to the sharply pointed tip (Fig. 1d). Spoon-tipped setae are more numerous in each cluster.

The endopod of the second maxilliped has sharply pointed serrate setae distally on the dactylus, whereas spoon-tipped serrate setae occur on the upper margins of the dactylus and propodus (Fig. 1e). *Favicola* has fewer setae than the other two species.

The basipodite of the first maxilliped has serrate setae on the inner margin (Fig. 1f).

Maxillae.—The first maxilla is a fingerlike process with simple setae distally (Fig. 1g). The protopodite of the second maxilla is undivided and has serrate setae on the inner margin in *Hapalocarcinus* and *Utinomia* (Fig. 1g). These setae are longer dorsally, decreasing in length ventrally. *Favicola* has multiple rows of conical tubercles along the inner margin and two serrate setae and one simple seta dorsally (Fig. 1h).

Gastric Mill. — Only the urocardiac and zygocardiac ossicles are present. All three species have similar median teeth, each consisting of two lateral rows of setiform projections separated by a narrow region of shorter projections or scales (Fig. 2a). The lateral teeth are entirely setiform in *Favicola* (Fig. 2b); mostly setiform, but with bluntly rounded papillae in *Hapalocarcinus* (Fig. 2c); and mostly setiform with rounded "cusps" in *Utinomia* (Fig. 2d).

DISCUSSION

None of the cryptochirid species studied has the classical filter-feeding setal net described by Marshall and Orr (1960). Filtering nets found among decapods include the plumose third maxillipeds of porcellanids (Nicol, 1932; Caine, 1975), the plumose antennae of *Paguritta* (see Schuhmacher, 1977), or the plumose net on the chelae of *Atya* (see Felgenhauer and Abele, 1983b). The only feeding structures of gall crabs are the pincerlike chelae and the third maxillipeds which have simple or serrate setae.

Plumose nets may be used for deposit feeding by porcellanids (Kropp, 1981) or atyids (Felgenhauer and Abele, 1983b), but most deposit-feeding decapods use

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Fig. 2. a, Utinomia dimorpha, gastric mill; b, Favicola rugosa, median tooth of gastric mill; c, F. rugosa, right lateral tooth of gastric mill; d, U. dimorpha, left lateral tooth of gastric mill; e, Hapalocarcinus marsupialis, left lateral tooth of gastric mill; f, Trapezia ferruginea, right lateral tooth of gastric mill. Scales: $a = 200 \ \mu m$; b, $c = 100 \ \mu m$; $d-f = 50 \ \mu m$.

a nonplumose feeding structure. Ocypodid crabs have spoon-shaped setae on the first and second maxillipeds (Miller, 1961; Vogel, 1984) and hermit crabs have simple or serrate setae on the maxillipeds (Kunze and Anderson, 1979). Farmer (1974) suggested that simple and serrate setae may be used for gripping food. The maxillipeds of gall crabs are appropriate for gathering soft detrital material such as coral mucus. These maxillipeds are similar to those of *Trapezia*, also a mucus feeder (Knudsen, 1967).

The teeth of the gastric mills of the three cryptochirid species differ from those of other crabs. For example, the typically brachyuran lateral teeth of *Trapezia* consist of two or three anterior cusps and a posterior series of transverse, flattened ridges (Fig. 2e), whereas gall crabs have mostly setiform lateral teeth. This contrast between crabs feeding on the same type of food may support the idea that phylogeny determines mill structure more than diet (Felgenhauer and Abele, 1983a). However, cryptochirids show variation from lateral teeth having what may be remnant cusps and setiform projections (*Utinomia*) to teeth lacking cusps altogether (*Favicola* and *Hapalocarcinus*). *Utinomia*, by feeding in a debris-filled border zone, may ingest coarse particles and has relatively robust lateral teeth. *Hapalocarcinus*, feeding on relatively pure mucus inside the gall, has setiform lateral teeth. However, *Favicola* may also ingest coarse material, but has setiform lateral teeth. The relative role of phylogenetic relationship or diet to the structure of the gastric mill remains unclear in this case.

My observations show that gall crabs collect food, including coral mucus and tissue, from the surface of the host. No filter feeding was observed, but it is possible that maxilliped fanning could have been misinterpreted by others as filter feeding. Fanning did not pull particles from the water column, but drew mucous strings to the mouth.

Many animals feed on living corals, some inflicting serious damage (Chesher, 1969; Moyer *et al.*, 1982). Coral mucus is an important food item for organisms such as bacteria (Ducklow and Mitchell, 1979b), zooplankton (Johannes, 1967; Richman *et al.*, 1975), molluscs (Robertson, 1970), crustaceans (Knudsen, 1967), and fish (Benson and Muscatine, 1974).

Uncontaminated mucus consists primarily of acidic mucopolysaccharides (Goreau, 1956) and wax esters (Benson and Muscatine, 1974; Benson *et al.*, 1978). Daumas and Thomassin (1977) and Ducklow and Mitchell (1979a) found glycine, serine, glutamic acid, and aspartic acid to be the most abundant amino acids in coral mucus. Krupp (1982) cautioned that pure coral mucus may be a poor nutrient source, at least in the case of *Fungia scutaria*. However, coral mucus rapidly becomes contaminated with organic material, resulting in a mucus high in nitrogen and phosphorus (Coles and Strathmann, 1973; Benson *et al.*, 1978; Ducklow and Mitchell, 1979a). *Utinomia* and *Favicola* feed on contaminated mucus from border zones. Therefore, studies of purified mucus or of mucus taken from whole colonies do not accurately estimate the dietary intake of these mucus feeders. Coral mucus may represent a detrital food pathway along which the products of photosynthesis by coral-associated zooxanthellae can be transferred to other members of the reef community.

Since gall crabs feed on their hosts, it is tempting to consider them as parasites. Corals, however, continuously exude mucus as part of a sediment rejection system (Abe, 1938). Therefore, ingestion of mucus by cryptochirids does not represent a metabolic drain on the host. Other effects of gall crabs on corals are unknown and represent future research possibilities.

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