AN ABSTRACT OF THE THESIS OF Roy K. Kropp for the Master of Science in Biology presented August 13, 1981.

Title: Feeding Biology of Three Hapalocarcinid Crab Species.

APPROVED: Lucius G. Eldredge

Lucius G. Eldredge, Chairman, Thesis Committee

The maxillipeds of three hapalocarcinid crab species--Hapalocarcinus marsupialis, Pseudocryptochirus kahe, and Favicola rugosus--previously thought to be filter feeders, were found to have long simple, serrate, or long spinose setae; not the plumose setae required for filter feeding. P. kahe was observed to obtain food by picking debris from the border zone around the pit, inside the pit itself, or from the coral surface. It also used its chelae to scoop mucus to the mouth. F. rugosus, by using a criss-cross chelae pattern, collected mucus and debris into a bolus which was eventually transferred to the mouth. H. marsupialis gathered mucus by rapid fanning of the third maxillipeds and by scratching the dactyls of its walking legs against the coral surface. Physiological studies were used to calculate O:N ratios of 121.1 for H. marsupialis and 62.4 for P. kahe. These high ratios indicate that the diet of each crab was high in carbohydrate and low in protein. The difference between the two relates to habitat-related food differences--P. kahe consumed mucus which was more likely to have accumulated debris. Mucus consumed by these crabs was not a metabolic drain on the coral because it is sloughed off normally as a part of the sediment-rejection system of the coral.

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FEEDING BIOLOGY OF THREE HAPALOCARCINID CRAB SPECIES

by

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INTRODUCTION

Most decapods which dwell within the coral skeleton belong to the brachyuran family Hapalocarcinidae. The family is widely distributed in tropical waters. The majority of the species in the family occur in the Indo-West Pacific (Castro, 1976; Takeda and Tomura, 1979). Two species are found in the East Pacific (Castro, 1979) and three are found in the Caribbean (Castro, 1976; Shaw and Hopkins, 1977). Hapalocarcinids are reasonably host specific, a feature that is the basis for the present taxonomic status of the group (Serene, 1967; McCain and Coles, 1979).

Although members of the family have been known for over 100 years, hapalocarcinid feeding biology has been little studied and is poorly known. Stimpson (1859), who described Hapalocarcinus marsupialis, thought that the species was free-living but fed on coral polyps. Verrill (1867) described the relationship between symboint and host as parasitic. Henderson (1906) discounted Stimpson's notion that Hapalocarcinus feeds on coral tissue by stating that living polyps exist within the gall. Potts (1915) presumed that gall crabs fed on plankton, specifically nannoplankton drawn through the holes in the gall by the respiratory currents of the crab. Stomach content analyses performed by Potts were inconclusive. Potts' ideas were cited by other authors for the next 60 years (Hiro, 1937; Marshall and Orr, 1960; Barry, 1965; Patton, 1967; Castro, 1976). Barry (1965) stated that other coral commensals feed on corals yet maintained that Hapalocarcinus does not receive any nourishment from its host.

There is now some indication 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. Gore (1980) mentioned that Troglocarcinus corallicola fed on coral mucus, and Kropp (1980) observed that Pseudocryptochirus kahe picked up particulate matter from the surface of the host coral. Therefore it is possible that hapalocarcinids obtain some of their nutritional requirements from the host coral.

Coral mucus has been shown to be an important food item for bacteria (Ducklow and Mitchell, 1979b), zooplankton (Johannes, 1967; Richman et al., 1975), molluscs (Robertson, 1970), crustaceans (Knudsen, 1967; Preston, 1971), and fish (Benson and Muscatine, 1974). Coral mucus may represent a detrital food pathway along which the products of photosynthesis by coral-associated zooxanthellae may be transferred to other members of the reef community.

The composition of mucus has been determined for a few coral species. Uncontaminated mucus consists primarily of acidic mucopolysaccharides (Goreau, 1956), triglycerides, 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. Additionally, contaminated coral mucus is high in nitrogen and phosphorus (Benson et al., 1978; Ducklow and Mitchell, 1979a), both of which are low in other forms of detritus (Fenchell and Jorgensen, 1977).

The purpose of this study was to clarify hapalocarcinid feeding biology. Anatomical studies were used to determine what type of food gathering apparatus is available to the crabs. Studies of behavior

enabled feeding motions to be described. Metabolic studies provided information about hapalocarcinid diet. Evidence from these studies showed that hapalocarcinids do not filter feed but collect food from their host corals.

STUDY ANIMALS

Female Hapalocarcinus marsupialis Stimpson, 1859 live in well-formed galls in many pocilloporid corals. Males are much smaller than females and are apparently free-living on host corals (Fize, 1956; MacNamee, 1961). In addition to hosts listed by Fize and Serene (1957), H. marsupialis occurs on Pocillopora danae, P. setchelli, and Seriatopora crassa (pers. obs.). It ranges throughout the tropical Indo-Pacific (Castro, 1976).

Pseudocryptochirus kahe McCain and Coles, 1979 inhabits pits in stoutly branched pocilloporid corals. It is known to occur in Pocillopora meandrina and P. eydouxi (McCain and Coles, 1979). This species resembles Cryptochirus dimorphus Henderson, 1906 and may be synonymous. Attempts to locate the types of C. dimorphus have been unsuccessful. The two appear to be very similar in anatomy and in the habit of the female occasionally holding a male within the abdominal pouch. P. kahe is known from Hawaii (McCain and Coles, 1979), Kosrae (Eldredge et al., 1979), Taiwan, Guam, and the Northern Marianas (pers. obs.).

Favicola rugosus (Edmondson, 1933) lives in pits formed in colonies of faviid corals. This crab was described living in pits in Favia speciosa. The species is also reported as living on Platygyra lamellina, P. daedalea, and Goniastrea aspera (Fize and Serene, 1957). At Guam F. rugosus occurs on Leptoria phrygia. It is known from Washington Island (Edmondson, 1933), VietNam (Fize and Serene, 1957), and Guam.

METHODS

Collection Sites

Galls containing female Hapalocarcinus marsupialis were collected from Pocillopora damicornis colonies in shallow water at Hotel Reef, Apra Harbor, Guam. Pieces of coral containing Pseudocryptochirus kahe were collected from colonies of Pocillopora eydouxi at a depth of 5-7 m on the reef front at Luminao Reef, Guam. Pieces of Leptoria phrygia housing Favicola rugosus were also collected from the reef front at Luminao. Specimens were returned to the laboratory and held in a large flow-through, partially shaded seawater tank (temperature 27.5±1.0°C) until used in one of the subsequent studies.

Food Gathering Appendages

The third, second, and first maxillipeds, and the dactyls of each walking leg of adult females were dissected from recently collected specimens of each species. Each was examined with both dissection and compound microscopes. Scanning election micrographs (SEM) of some mouthparts were made. Types of setae on each mouthpart were determined and drawings of each appendage were made using a Ken-A-vision micro-projector. Setal types were classified according to the system used by Kunze and Anderson (1979).

Behavior

I used a dissection microscope to observe feeding behavior of crabs in their dwellings on small pieces of coral. The growing edge of Hapalocarcinus galls was removed to allow observation of adult female

crabs. Light from the microscope illuminator had no noticeable effect on crab behavior.

Crab behavior was observed for 14 twenty-minute periods during which feeding activities were recorded and described. These data were used to categorize feeding behavior. Subsequently, crabs were observed for two successive ten-minute periods during which the category of each distinct feeding action was recorded. These data were used to estimate the frequency of occurrence of each feeding category.

The consequences of feeding motions were determined by dropping carmine onto the coral's surface adjacent to the pit or gall.

Metabolic Studies

Immediately before metabolic studies, I removed crabs from their galls or pits, rinsed them in 0.45 μ filtered seawater (FSW) and placed them in an appropriate reaction vessel. After each trial crabs were sacrificed by chilling, the eggs removed from each ovigerous female (any P. kahe males present were also removed). Crabs and eggs were rinsed with distilled water and dried at 50°C for 24 h, cooled to room temperature in a desiccator, and weighed to nearest 0.1 mg. F. rugosus was not used in the metabolic studies because of the difficulty in obtaining sufficient numbers with which to work.

Ammonia Excretion

Crabs to be tested were placed in vials containing 12 ml of FSW. A 5 ml pre-sample was removed from each vial. Ammonia concentration of each sample was determined with an Orion model 95-10 gas-sensing ammonia electrode attached to an Orion Ionalyzer/901. Ammonia excretion was expressed as mg NH_4^+-N·g^{-1}·h^{-1}.

Respiration

Crab respiration rates were determined by using a Gilson differential respirometer at 28.0±0.1°C and the slowest shaking speed. Crabs were removed from their galls or pits, rinsed in FSW, placed in reaction flasks, and allowed to acclimate for 15 minutes. Readings were taken at 30-minute intervals. Egg mass O_2 consumption was determined by teasing eggs for several females and following the same procedure as for individual crabs. Respiration rates were calculated by the regression of O_2 consumption on time. Respiration rates of ovigerous females were corrected for egg respiration.

Chemical Analyses

Percent nitrogen of whole crabs was determined using the microkjeldahl procedure with arginine hydrochloride as a standard. Caloric content of whole crabs was determined with a Phillipson microbomb calorimeter (Gentry, Inc.).

RESULTS

Dwellings

The galls in which H. marsupialis dwells have been thoroughly described (Potts, 1915; Hiro, 1937). The mature female crab is permanently encased within a well-formed coral skeleton gall. Water circulates through the gall via small holes along the suture line between upper and lower halves of the gall. Although there maybe some septal deformation (Hiro, 1937), the inside of the gall is lined with living coral tissue.

Pits made by P. kahe are recognizable from a distance as a pinkish purple spot on the coral branch. This color, of unknown origin, surrounds a circular or subcircular opening. The pit is surrounded by a border zone, in which there is no live coral tissue. Brown, flocculent debris usually accumulates within the border zone. On occasion, filamentous algae including Schizothrix mexicana, Hormothamnion sp., Anacystis sp., and Centroceras sp. occur within the zone. Diatoms may also be present here. Usually coral verrucae do not occur within the zone but frequently line the outer edge of the zone. In such cases the pitward side of the verruca is eroded. The border zone appears to be delimited by the distance away from the pit that the crab is able to reach and may extend to three millimeters from the pit edge.

Pits made by Favicula rugosus in Leptoria phrygia are circular and surrounded by a narrow border zone within which there is no living coral tissue. The coral around the pit is usually characterized by an alteration of calice growth so that the calice wall often completely surrounds the pit with the long axis of each septum perpendicular to the pit. The area surrounding a pit is often elevated above the normal coral surface.

Setae

Seven types of setae were found on hapalocarcinid mouthparts. These were placed in categories as described and illustrated by Kunze and Anderson (1979). A list of setal types, numbered as in Kunze and Anderson (type 3, comb setae, was not found) follows:

1. Long, simple setae--Long setae without setules or serrations, may be straight or curved (type g, 1 of Farmer, 1974).
2. Long, spinose setae--Long setae with two rows of fine setules (type a of Farmer).
4. Serrate setae--Long setae with two rows of relatively large cuneate setules (type c of farmer).
5. Pappose setae--Long setae with thin setules arising irregularly from all setal surfaces. Setules may be longer than length of a seta (type e, f, k of Farmer).
6. Plumose setae--Long setae with two rows of setules arising from the shaft (type j of Farmer).
7. Stout simple setae--Setae similar to type 1 but shorter and thicker (type h of Farmer).
8. Stout serrate setae--Setae similar to type 4 but shorter and thicker; may be slightly longer than indicated by Kunze and Anderson (type i of Farmer).

Mouthparts

Hapalocarcinus marsupialis

Third maxilliped (Fig. 1; Plate I)--The endopod is large and five segmented, the last four of which form a well-developed palp. The inner margin of the basi-ischium is sparsely setose on its lower half, having about 12-14 stout simple setae (7), whereas the upper half is more

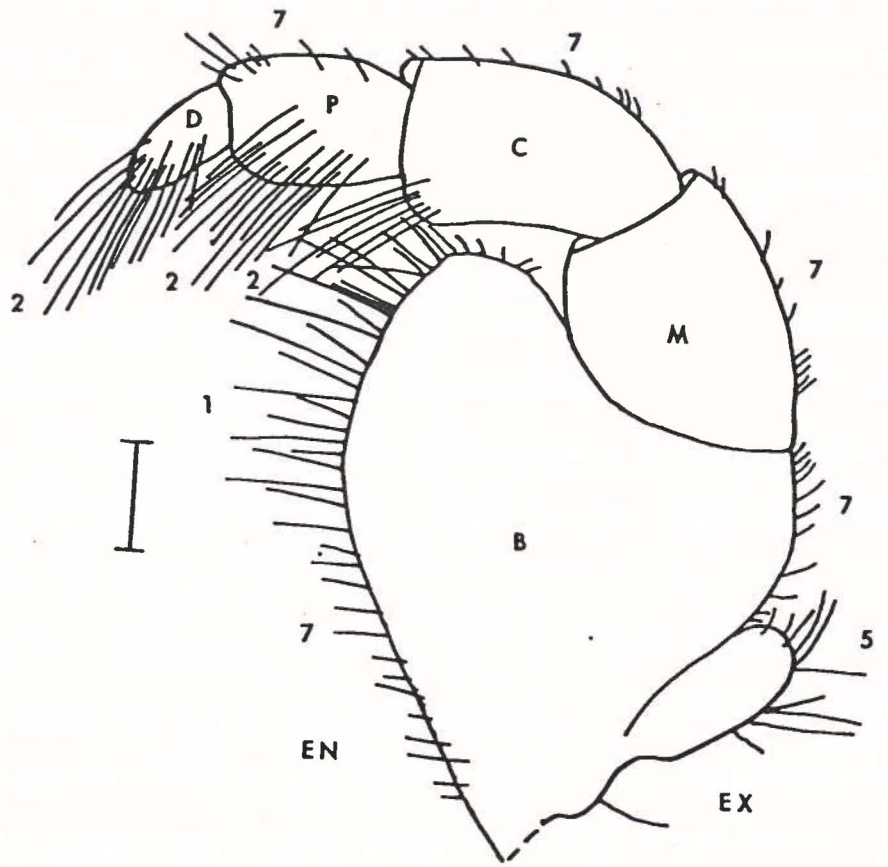

Figure 1. Left Third Maxilliped of H. marsupialis. [Abbreviations and Scale used for Figures 1-10: B-Basi-ischium; M-Merus; C-Carpus; P-Propodus; D-Dactyl; F-Flagellum; EN-Endopod; EX-Exopod. Numbers refer to Setal Type--see Text. Scale = 0.2 mm.]

setose, having about 18-20 long simple setae (1). The inner margin of the carpus has two clumps of 10-12 long spinose setae (2) arising from its distal half. The propodus has a patch of long spinose setae (2) arising from the distal two-thirds of its inner surface. The dactyl has a cluster of 20-30 long spinose setae (2) arising from its inner surface and tip.

Second maxilliped (Fig. 2; Plates II, III)--The endopod is five segmented. The upper surface of the propodus has 15-18 long simple setae (1) and about 22-26 long simple setae (1) arise from the upper surface and tip of the dactyl. The terminal segment of the exopod has a clump of plumose setae (6) on its upper surface.

First maxilliped (Fig. 3)--The tip of the slender proximal endite (not shown) has a few long simple setae (1). The wider distal endite is fringed with 20-22 long simple setae (1). The endopod has 16-20 widely spaced stout simple setae (7) on its inner margin. The distal tip of the flagellum has 26-30 plumose setae (6) on its upper surface.

Walking legs (Fig. 4)--All four walking leg pairs are similar in size and structure. The dactyl is smooth and has many, scattered long simple setae (1). These setae differ from the usual type found on the maxillipeds by being strongly curved distally. Setae occur on all surfaces of the dactyl except the tip. The propodus is similar, being smooth and having many "hooked" long simple setae (1). These setae are longest and most numerous at the antero-distal corner of propodus. The carpus and merus are smooth and sparsely setose.

Pseudocryptochirus kahe

Third maxilliped (Fig. 5; Plate IV)--The endopod is morphologically similar to that of H. marsupialis. The inner margin of the basi-ischium

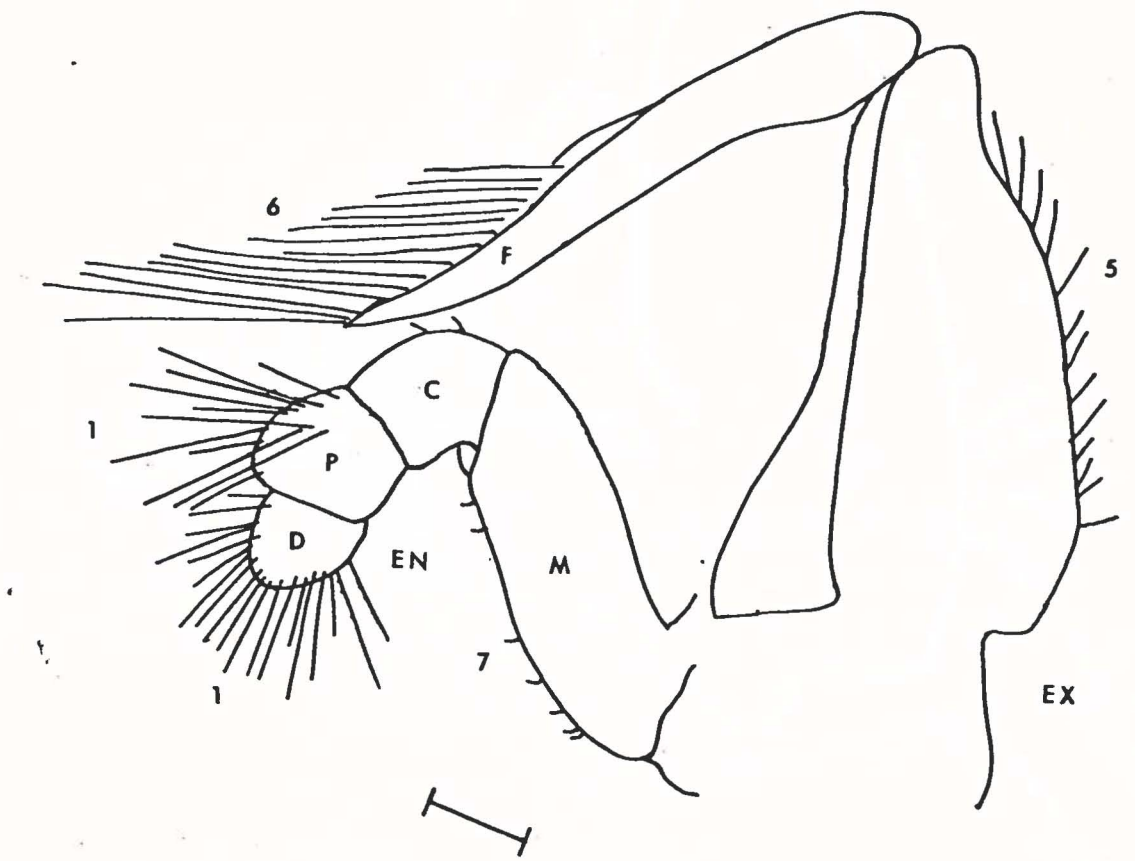

Figure 2. Left Second Maxilliped of H. marsupialis.

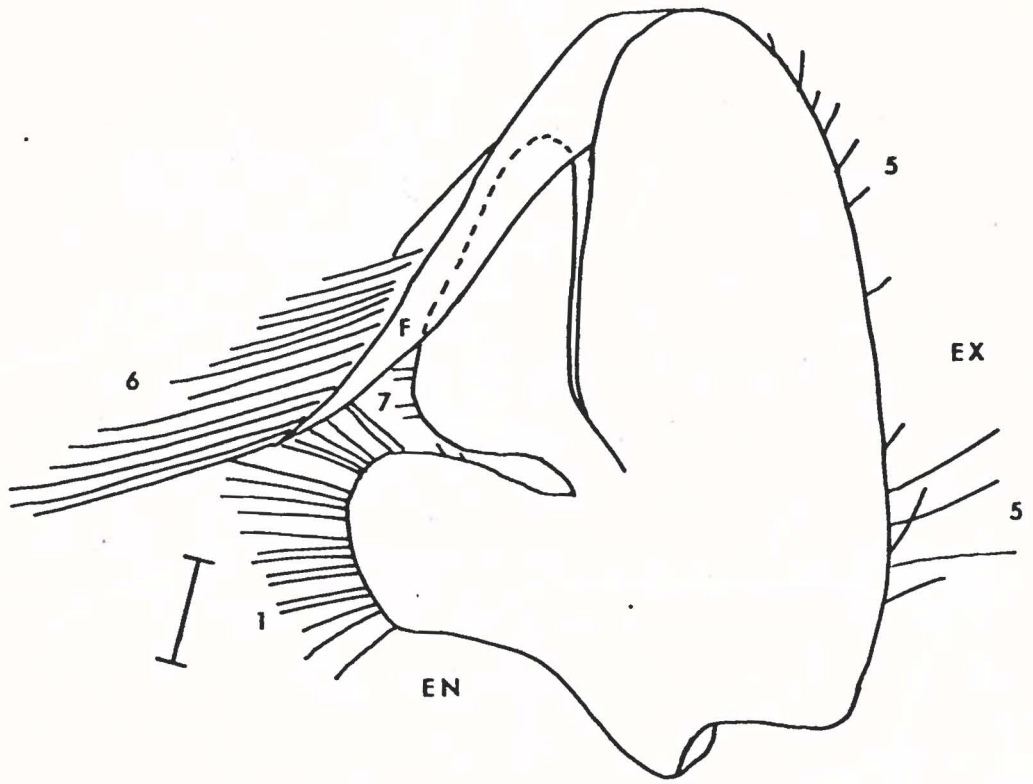

Figure 3. Left First Maxilliped of H. marsupialis.

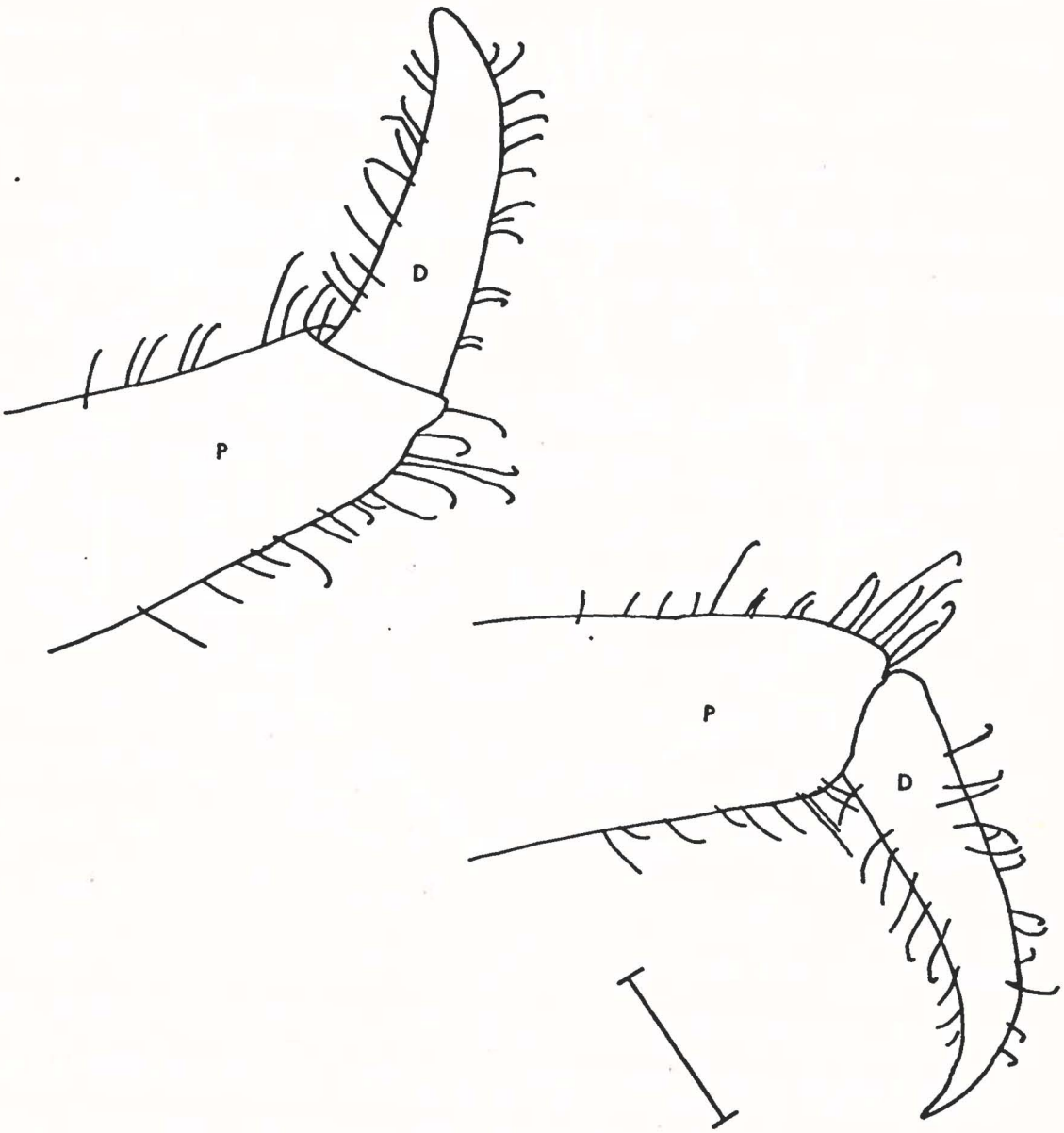

Figure 4. Walking Leg Dactyls of H. marsupialis. Shown are Left First (top left) and Second (bottom right) Legs.

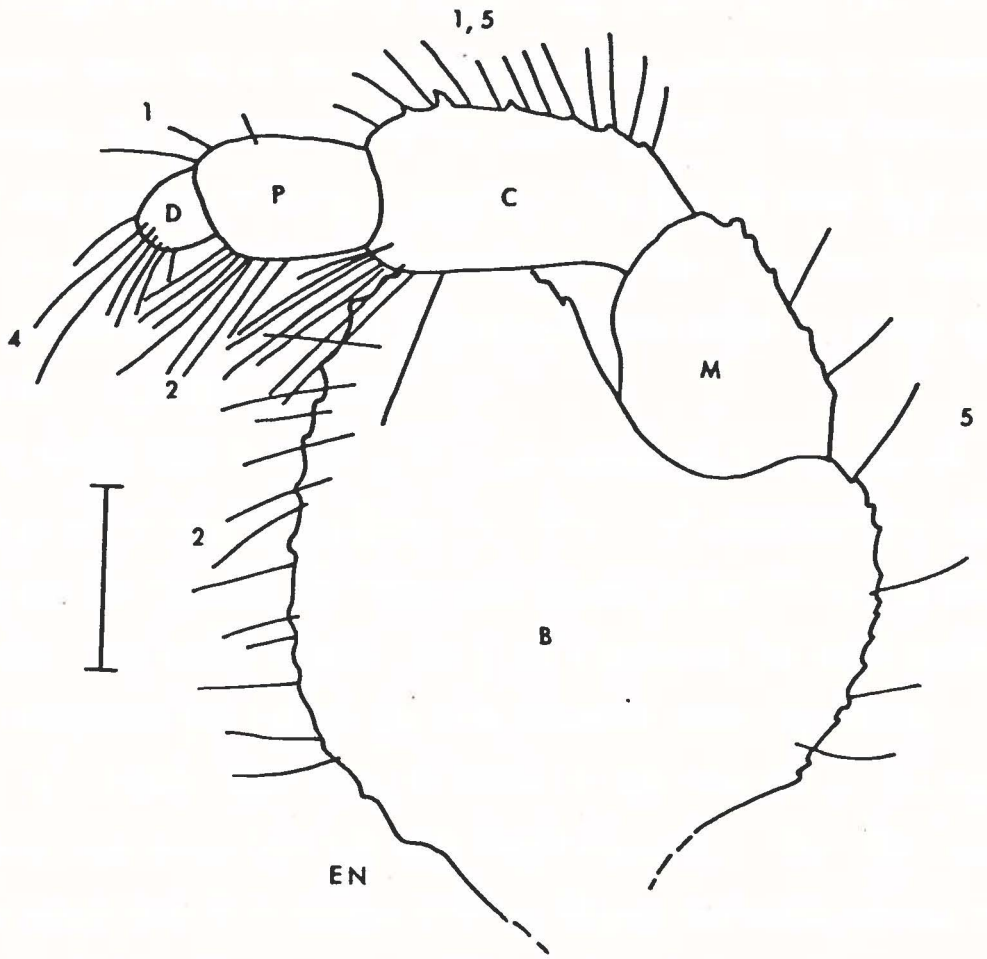

Figure 5. Left Third Maxilliped of P. kahe.

is fringed with 12-16 widely spaced long spinose setae (2). The few pappose setae (5) on the outer margin of the merus may be covered with diatoms. The outer margin of the carpus has 10-12 long simple setae (1) and pappose setae (5). Several of the pappose setae have very long setules. Diatoms may be attached to the setae. The inner surface of the carpus has a cluster of 8-10 long spinose setae (2) which arise from the distal corner.

Second maxilliped (Fig. 6)--The endopod is five segmented. The tip and outer surface of the dactyl has 20-24 long stout serrate setae (8). The proximal segment has 18-20 long pappose setae (5) on its outer margin. The second segment has a few diatoms on its outer surface. The flagellum has a clump of 10-14 plummose setae (6) distally.

First maxilliped (Fig. 7; Plates V, VI)--The tip of the proximal endite (not shown) has 4-6 long simple setae (1). The inner surface of the distal endite is fringed with 10-14 long and thick serrate setae (4). The flagellum has a few plumose setae (6) distally.

Walking legs--The first walking (Fig. 8) leg is the largest of the four. The dactyl is curved, smooth, and virtually hairless. The propodus is sparsely setose, having scattered along simple setae (1) and pappose setae (5). The carpus and merus are similar to the propodus. The second walking leg is relatively small. The dactyl is smooth and mostly hairless. The propodus has scattered pappose setae (5) and some long simple setae (1). The carpus and merus are similar to the propodus. The third and fourth walking legs are similar to the second.

Favicola rugosus

Third maxilliped (Fig. 9)--The inner margin of the endopod basiischium has two rows of 12-14 regularly spaced long simple setae (1).

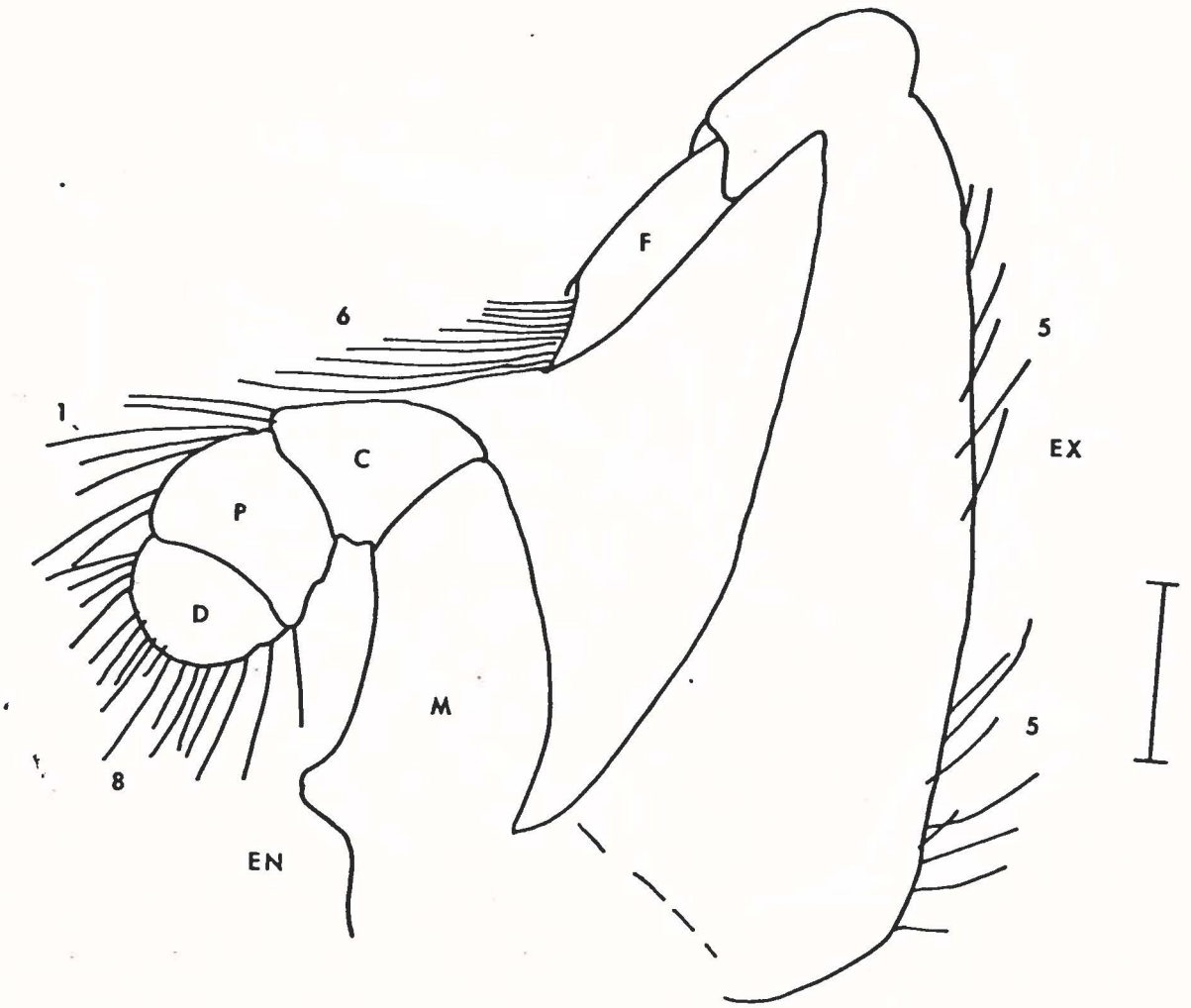

Figure 6. Left Second Maxilliped of P. kahe.

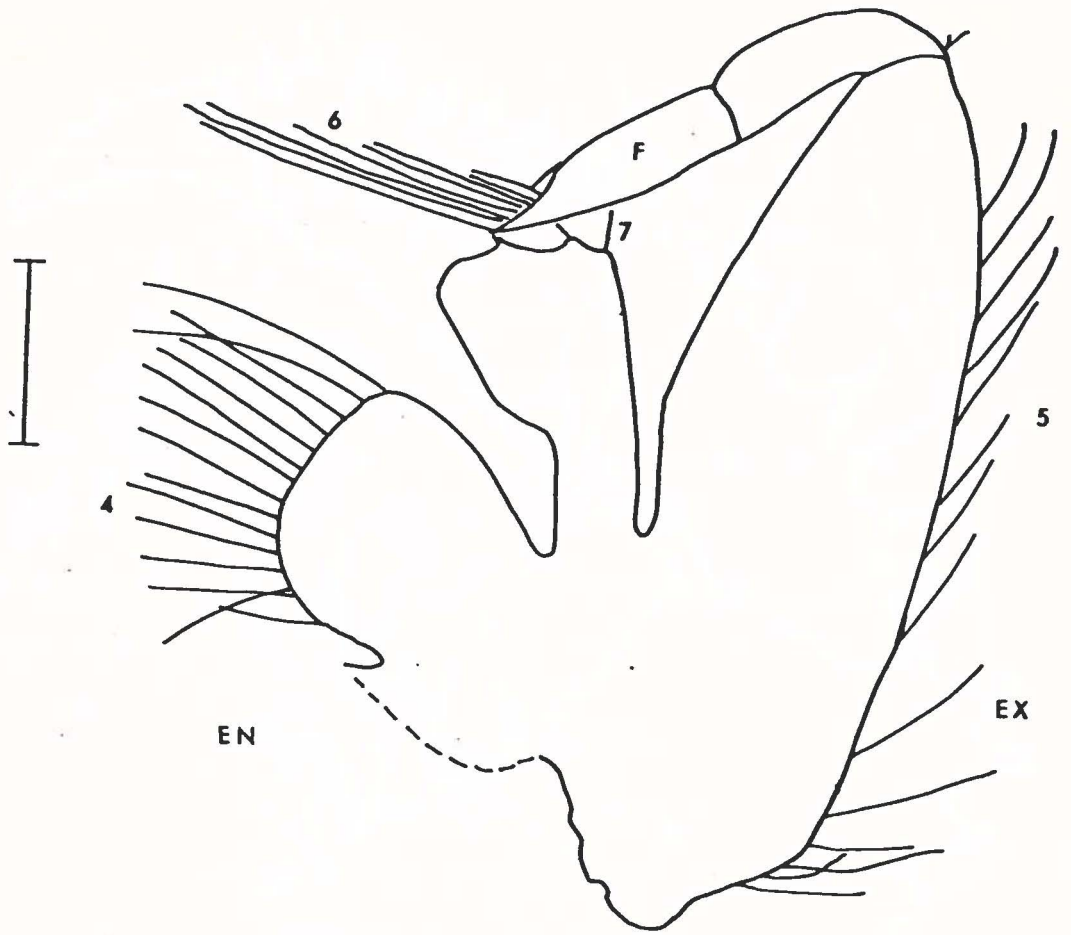

Figure 7. Left First Maxilliped of P. kahe.

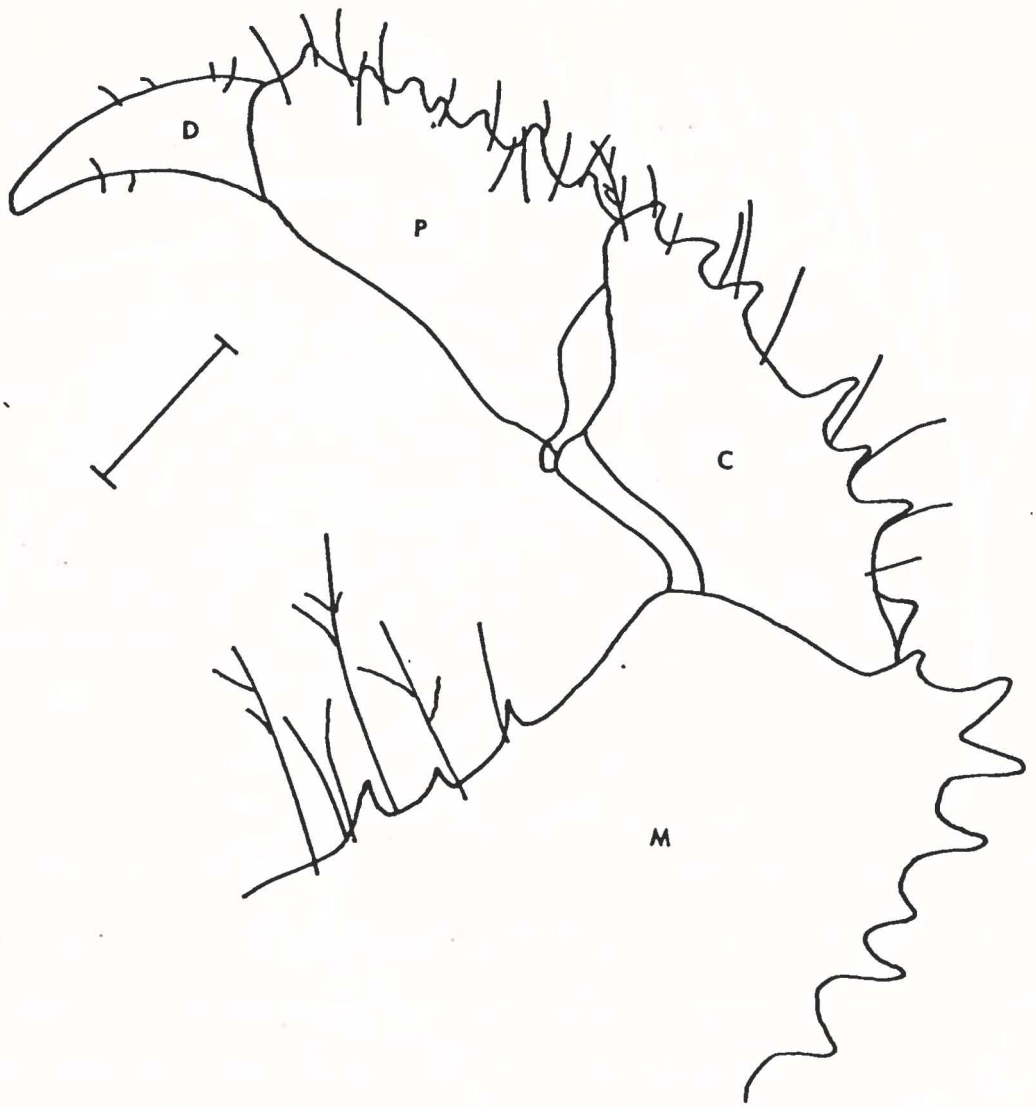

Figure 8. Left First Walking Leg of P. kahe.

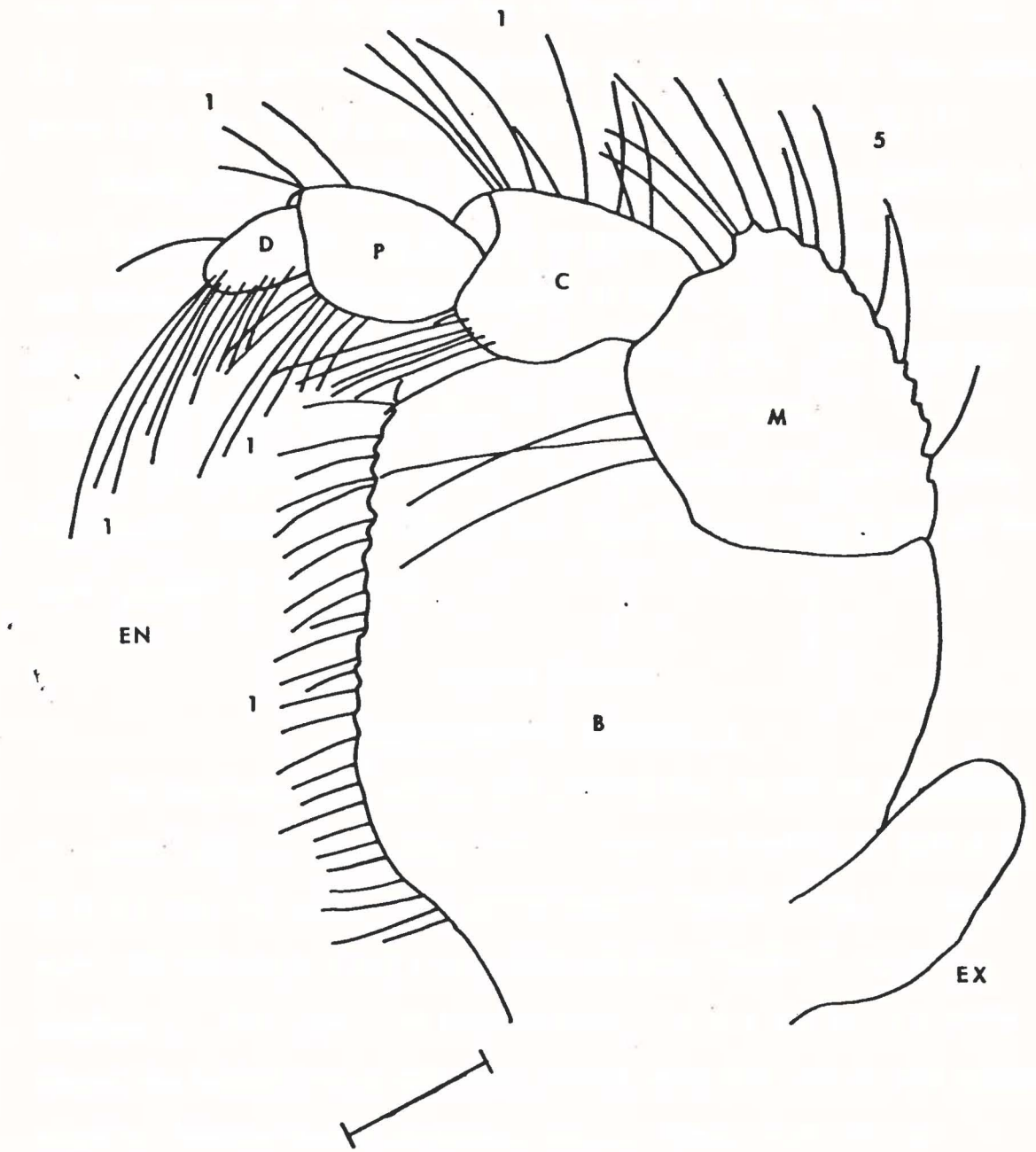

Figure 9. Left Third Maxilliped of F. rugosus.

The inner margin of the carpus has a clump of 6-10 long simple setae (1). The inner surface of the propodus has a clump of 7-10 long simple setae (1). The tip of the dactyl has 10-14 long simple setae (1).

Second maxilliped (Fig. 10)--The upper surface of the dactyl has 8-12 long simple setae (1) and the tip has 14-18 stout setae (8) which are unusually long. The basal segment of the exopod has 14-16 pappose setae (5) the distal 3-4 of which are extremely long. The flagellum has a clump of 6-8 plumose setae (6) on its upper surface.

First maxilliped (not shown)--This appendage is sparsely setose, having only plumose setae (6) on the flagellum and outer margin of the basal segment of the exopod.

Feeding Behavior

Hapalocarcinus marsupialis

The chelipeds were used as the primary food gathering appendages in several ways. They grasped coral tissue from inside the gall and pulled it to the mouth. They picked debris (mucous flocs) off the coral surface and off the crab's body and transferred it to the mouthparts. The claws also scooped material along the coral surface toward the buccal cavity and also reached under the ventrum and scooped material forward toward the buccal cavity. Mucus occasionally accumulated on the chelipeds and was wiped off by the maxillipeds.

The third maxillipeds frequently swept the area in front of the buccal cavity. This action occurred primarily in a plane parallel to the buccal cavity. Sweeping began as a lateral movement of the basal endopod segments moved medially, the palp was rapidly flexed toward the

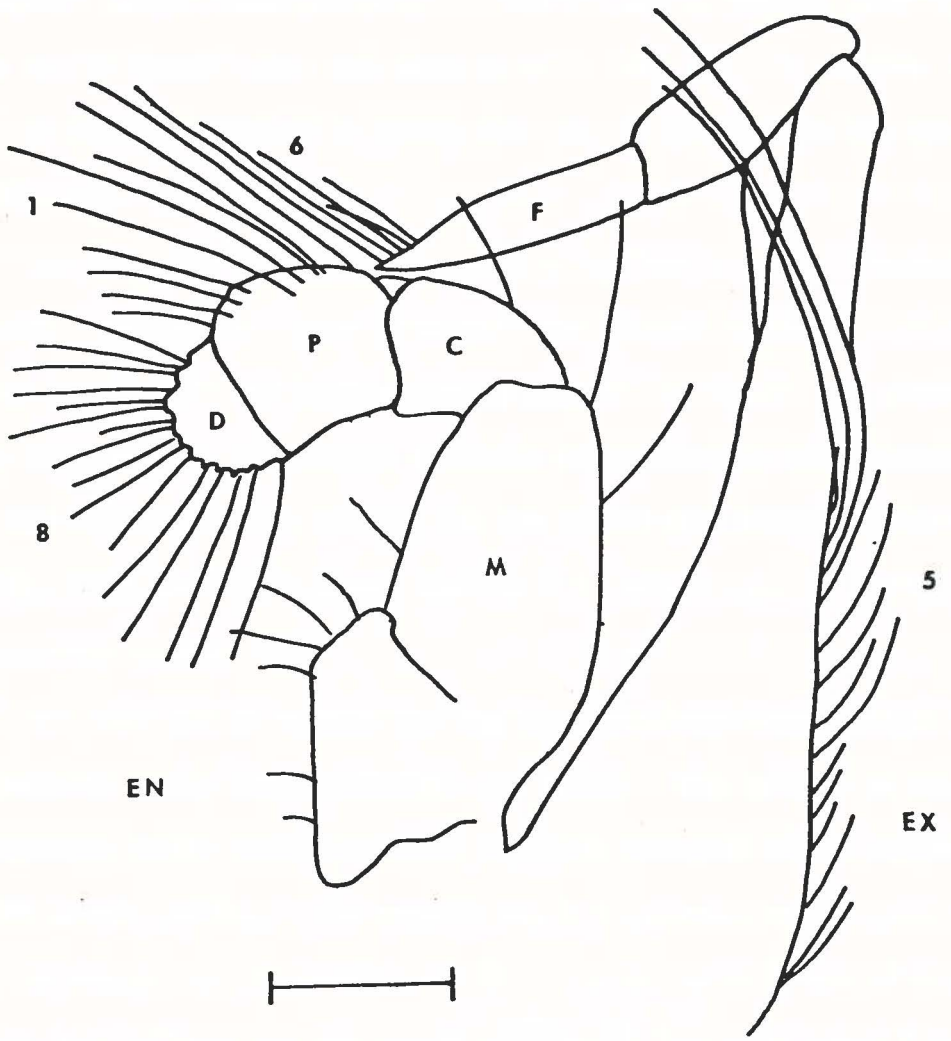

Figure 10. Left Second Maxilliped of F. rugosus.

buccal cavity. Usually the third maxillipeds fanned alternately but sometimes fanned simultaneously. Fanning bouts brought carmine particles to the buccal area and were usually less than 30 seconds long. Fanning was accompanied by occasional quick cheliped pokes toward the mouth area.

The third maxillipeds also made a variety of other movements. They reached down one at a time with the palp to the lower part of the buccal cavity (or lower) and pushed inward toward the mouth. In another pattern, one or both palps were extended to an area on the carapace behind the eye and swept down across the eye toward the buccal cavity. Similarly, palps were also swept down in a circular pattern across the second maxillipeds.

All four pairs of walking legs performed movements which resulted in material being transported to the mouth. The primary action involved a vigorous, rapid shaking of the leg in a vertical plane perpendicular to the coral surface. The result was a vigorous scratching of the walking leg dactyl on the coral surface. Following a series of shaking bouts, the walking leg was moved underneath the body where flocculent material was picked off the dactyl by a cheliped. The cheliped then transferred the material to the mouthparts. Shaking usually occurred one leg at a time.

Sometimes, after a shaking bout, the dactyls of two adjacent walking legs were vigorously rubbed together. This action caused material, which had accumulated on the dactyls, to break apart and be cast into the water adjacent to the crab. This material was pulled into the buccal cavity by mouthpart activity. Less vigorous dactyl rubbing which did not cause accumulated material to break apart, also occurred.

Following this rubbing, a walking leg was placed under the crab body and material cleaned off the dactyl by a cheliped. The material was then transferred to the mouthparts.

Walking leg dactyls were also slowly rubbed against coral tissue on the upper gall surface. These bouts lasted about 15-20 sec and were followed by cleaning of the dactyl by a cheliped and transfer of material to the mouthparts. Dactyls also poked at coral tissue, without scratching, then scooped toward the body.

After carmine particles had been placed in the gall, all of the previous movements caused carmine-mucus strings to accumulate on the walking leg dactyls and eventually to be transported to the mouth.

During 19 ten-minute observation periods, H. marsupialis made 52.1±9.0 feeding related actions per period. Rapid maxilliped fanning occurred 25.1±5.6 times; walking leg shaking or scratching occurred 13.5±7.2 times; cheliped scooping happened 11.0±7.0 times; and cheliped snips at the body took place 2.4±2.0 times per period.

Pseudochryptochirus kahe

The chelipeds were used by P. kahe to snip at various objects both inside and outside the burrow and subsequently transfer material to the buccal cavity. Snips inside the pit were directed at loose material (debris) which had accumulated either on the crab itself or within the pit. Snips were directed toward several regions of the body including the abdominal pouch, eyes, and carapace. Also debris was snipped from the inner wall of the pit and from within the border zone. This material included debris, mucous strands, or algae. Occasionally crabs reached beyond the border zone to collect food, usually coral tissue.

Small pieces of coral tissue were snipped from the edge of the coenosteum fringing the border zone or from coral polyps.

The chelipeds were also used several ways by P. kahe to scoop mucous strands toward the buccal cavity. Usually scooping began by extension of the chela (with the fingers closed) into the border zone. The fingers of hand were opened then poked one or several times onto the border zone substrate or onto coral tissue. Following this poking the chela was quickly flexed toward the mouth with the fingers agape. A slight modification of this method involved a squeezing of coral tissue by the fingers of the chela but without extraction of coral tissue. The chela was then quickly flexed to the mouth as before. Similar scoops were also directed into the water column above the pit or border zone. Both types of scooping were followed by rapid fanning of the third and second maxillipeds. Crabs were seen to sweep one cheliped over the other to remove debris. A similar action was directed toward the postorbital region of the carapace.

Carmine particles were quickly picked up by mucus and formed into long strings. Many carmine-mucus strings moved toward the pit. At the outer edge of the border zone the strings stopped horizontal movement and piled up into the water column above the zone. The scooping movements of the chelae into the border zone and water column pulled these carmine-mucus strings toward the mouth. Maxilliped fanning helped pull the strings to the mouth. Carmine-mucus strings often caught on the chelipeds and carapace and were cleaned off by chelae scoops directed toward those areas.

Rarely, the chelipeds were used in a criss-cross fashion to pull mucus into a bolus which was eventually taken to the mouth and

manipulated by the outer maxillipeds. Crabs were observed to hold a bolus of mucus (and debris) in the fingers of one chela. This chela was then moved backwards along the edge of the pit and then brought forward to the portion of the pit directly opposite the midline of the body. The bolus was then transferred to the fingers of the other chela which subsequently moved backwards along the pit rim and then forward to the midline. This exchange occurred any number of times whereupon the bolus was taken to the mouth and manipulated by the maxillipeds for a brief period. One chela then removed the bolus from the mouthparts and the criss-cross pattern was repeated again.

The third maxillipeds were observed to fan rapidly, independent of any cheliped action. This fanning, which occurred in a plane parallel to the buccal cavity, did not pull any carmine-mucus strings into the mouth area.

The walking legs did not make any movements that resulted in material being transported to the mouth.

The results of the 28 ten-minute observation periods showed that 42.4±13.2 feeding related actions were performed per period. Cheliped snipping at the border zone, within the pit, or at the crab body occurred 25.8±10.9 times; scooping into the border zone, into the water column, or at the body occurred 9.9±5.5 times; and rapid maxilliped fanning occurred 6.7±4.4 times per period.

Favicola rugosus

Other than one instance when a crab grabbed a piece of coral tissue and ingested it, only one method of food gathering by Favicola rugosus was observed. In this method the claws were used to draw mucus into a bolus which was eventually transferred to the mouth. With the left

chela, for example, holding a bolus of mucus and debris at the edge of the pit directly in front of the crab, the right chela moved over to the left chela. The fingers of the right chela were placed around the left chela proximal to the bolus. The right chela then moved distally along the left chela, pushing the bolus off the left chela. The right chela then grabbed the bolus and swept it backwards along the edge of the pit. The chela then returned along the pit edge to the front. During this action the left chela extended slightly back along the pit edge and then scooped forward. When the chelae met at the front of the pit, the bolus was either exchanged from one chela to the other and the process repeated or it was taken to the mouth. This criss-cross pattern was repeated from 2-31 times before the bolus was taken to the mouthparts.

Carmine particles placed near the pit quickly become incorporated into mucous strings. These strings moved up the sides of the septa and then along the top of the septa toward the pit. Carmine moved into the pit from all directions and was incorporated into the bolus as a result of both of the chelae movements.

The third maxillipeds held the bolus and slowly rotated it while the second maxilliped endopod repeatedly stabbed into the bolus. After a time one chela removed the bolus and began another criss-cross pattern. Sometimes the crab expelled the bolus after which a new bolus was formed. The bolus was formed by rapid scooping of the chelae from the coral surface toward the mouth accompanied by rapid third maxilliped fanning. Both actions pulled carmine-mucus strings to mouth area where a small bolus formed. This bolus was picked out by one chela which then began the criss-cross pattern. A new bolus was completely

formed within two minutes after experimental removal of the old bolus.

Metabolic Studies and Chemical Analyses

The results of the metabolic studies and chemical analyses are presented in Table 1. The values given are means ± standard deviations. Female H. marsupialis ranged from 7.7 to 21.6 mg dry weight for the excretion studies and 3.4 to 13.1 mg dry weight for the respiration studies. There was no significant correlation ($p<0.05$) between weight and either excretion rate ($r = -0.390$) or respiration rate ($r = -0.457$). Female P. kahe ranged from 2.9 to 8.0 mg dry weight for the excretion studies from 2.0 to 10.2 mg dry weight for the respiration studies. There was no significant correlation ($p<0.05$) between weight and either excretion rate ($r = -0.175$) or respiration rate ($r = -0.388$).

The mean excretion and respiration rates were used to calculate atomic O:N ratios for each species (Table 1). The metabolic rates and the chemical analyses were used to derive nitrogen and caloric turnover rates for each species. The nitrogen turnover rates ($\%\cdot day^{-1}$) were 4.8 for H. marsupialis and 15.5 for P. kahe. The caloric turnover rates ($\%\cdot day^{-1}$) were 3.8 for H. marsupialis and 6.6 for P. kahe.

Table 1. Results of metabolic studies and chemical analyses. Excretion rates are expressed as $mg \cdot g^{-1} \cdot h^{-1}$ and respiration rates as $\mu\ell \cdot mg^{-1} \cdot h^{-1}$.

	Excretion Rate	Respiration Rate	O:N	%N	Calories$\cdot g^{-1}$
H. marsupialis	0.016±0.015 (N=19)	1.52±0.31 (N=12)	121.1	7.8±0.2 (N=3)	4669.9±252.0 (N=3)
P. kahe	0.038±0.022 (N=21)	1.86±0.87 (N=13)	62.1	5.8±0.1 (N=3)	3240.5±209.4 (N=3)

DISCUSSION

None of the three hapalocarcinids studied possess classical crustacean feeding appendages as described by Marshall and Orr (1960). This classical filter is a setal net, each seta having two regular rows of setules arising from it. An outstanding example of these plumose setae can be found on the third maxillipeds of porcellanid crabs--well known anomuran filter feeders (Nicol, 1932; Wicksten, 1973; Caine, 1975). The numerous long plumose setae of porcellanids contrast with the relatively sparse, simple setae found on hapalocarcinid third maxillipeds.

Although some porcellanids deposit-feed by using their plumose third maxillipeds (Kropp, 1981), most deposit-feeding crustaceans employ nonplumose setae. Fiddler crabs, for example, have specialized spoon-tipped setae on the first and second maxillipeds (Miller, 1961) and hermit crabs have simple or serrate setae to collect detritus (Roberts, 1968; Kunze and Anderson, 1979). Farmer (1974) stated that simple and serrate setae may be used for gripping food particles. Hapalocarcinid mouthparts, which are similar in setation to those of Tetralia and Trapezia as described by Knudsen (1967), are appropriate for gathering detrital material such as coral mucus. However, Tetralia and Trapezia have well-developed setose food brushes which are used to collect mucus, on the walking leg dactyls, whereas Hapalocarcinus only has discrete, hooked setae.

All three hapalocarcinids collected material from the coral surface to use as food. The predominant feeding behavior of P. kahe involved use of chelae to pick up material from areas in and around the pit. F. rugosus, used a criss-cross pattern of the chelae almost

exclusively. This previously undescribed method collected material into a bolus from which food was extracted. H. marsupialis collected mucus from the coral surface by using walking leg scratching similar to that described by Knudsen (1967) for Tetralia and Trapezia.

The predominant feeding method of H. marsupialis involved rapid maxilliped fanning. This fanning might be interpreted as filter feeding but only pulled in carmine particles which had become incorporated into mucous strands. The other two hapalocarcinids infrequently used maxilliped fanning, which also pulled mucus to the mouth.

Data from the metabolic and chemical studies indicate that hapalocarcinids probably feed on a high carbohydrate and low protein food. The O:N ratio may be indicative of metabolic substrate utilization (Bayne et al., 1976). Capuzzo and Lancaster (1979), working with postlarval lobsters, found that the O:N ratios varied inversely with the amount of protein in the diet. Examples from their data are an O:N ratio of 12.9 for a diet which was 51 percent protein and a ratio of 23.3 for a diet having about 17 percent protein. Therefore, the O:N ratios measured here for H. marsupialis and P. kahe indicate a low protein, much less than 17 percent, high carbohydrate diet. Further, the difference in O:N ratios between the two species is indicative of habitat-related food differences. For example, P. kahe collects its food from a border zone in which debris accululates, whereas H. marsupialis collects its food from the living coral surface on which little debris accumulates. Therefore, because mucus gradually increases in nitrogen content as it becomes contaminated (Coles and Strathmann, 1973), the food of P. kahe probably has a higher nitrogen content than that of H. marsupialis.

Hapalocarcinid nitrogen turnover rates are similar to those reported for planktonic crustaceans. For example, calanoid copepod turnover rates ranged from 3.7 to 14.5 $\%\cdot day^{-1}$ (Butler et al., 1969). An increase in nitrogen content of the diet increases the nitrogen excretion rate and, therefore, the nitrogen turnover rate (Corner and Davies, 1971). Thus, the higher nitrogen turnover rate for P. kahe (15.5) than for H. marsupialis (4.8) is another indication that the diet of P. kahe has a higher nitrogen content.

The low caloric turnover rates for H. marsupialis (3.8) and P. kahe (6.6) indicate that the energy content is not a critical dietary factor for either species.

The data resulting from the metabolic rate studies should not be used to predict the chemical content of the mucus produced by an entire colony because they are based on intake of food from a localized area. For example, material collected in the border zone surrounding the pit of P. kahe probably alters the mucus composition there compared to that away from the pit. Similarly the content of mucus collected from whole colonies does not accurately estimate the dietary intake of mucus feeders.

The data presented here show that hapalocarcinids do not have the apparatus necessary to filter feed but collect food from the coral surface. The metabolic studies show that the diet, primarily detrital mucus, of hapalocarcinids is low in protein and high in carbohydrate. Because corals continuously exude mucus as part of a sediment rejection system (Abe, 1938), the ingestion of mucus by hapalocarcinids does not represent a metabolic drain on the host coral.

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Plate I. Palp Region of Left Third Maxilliped of H. marsupialis. 87X.

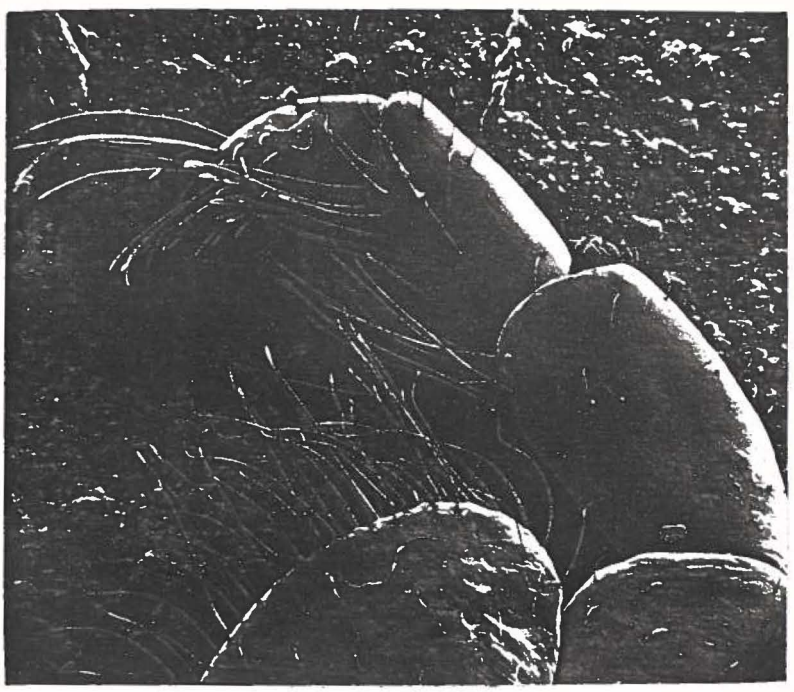

Plate II. Left Second Maxilliped of H. marsupialis. 43X.

Plate III. Endopod of Left Second Maxilliped of H. marsupialis. 85X.

Plate IV. Palp Region of Left Third Maxilliped of P. kahe. 178X.

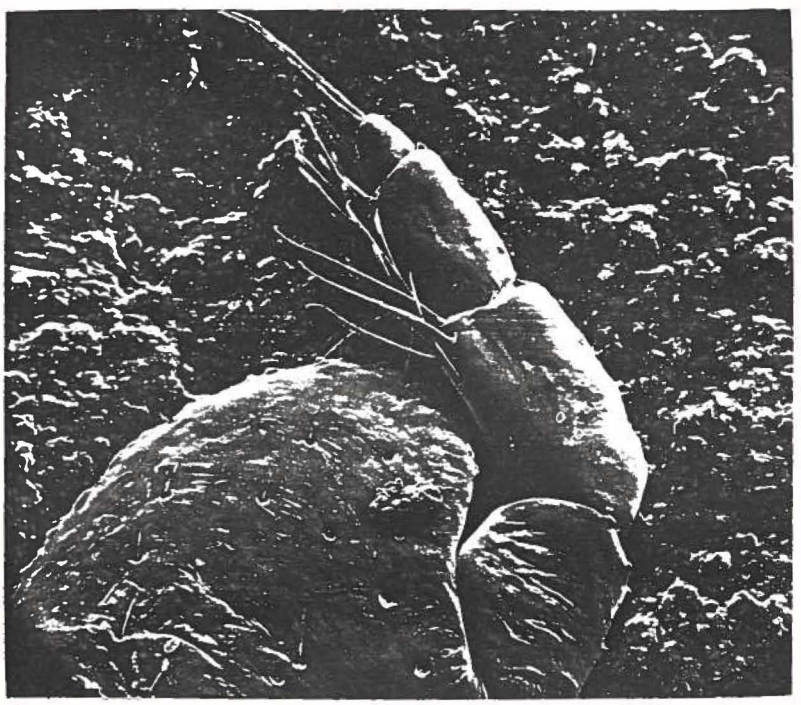

Plate V. Endopod of Left Second Maxilliped of P. kahe. 202.8X.

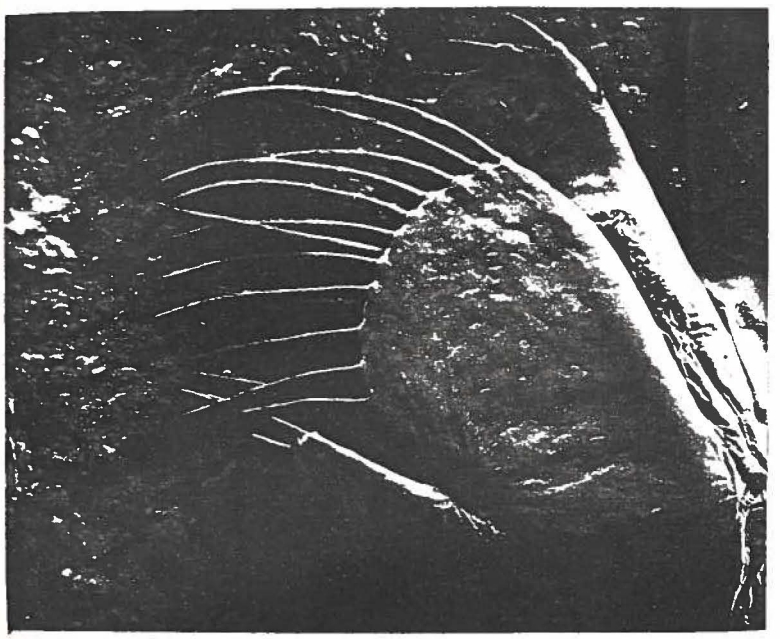

Plate VI. Left Second Maxilliped of P. kahe. 92.4X.