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Functional Morphology of Mouth Parts & Feeding Behaviour in the Estuarine Hermit Crab *Clibanarius longitarsus* (De Haan)

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C. longitarsus is largely an omnivorous detritus feeder. Scavenging and predation seem to be opportunistic. A detailed examination of the morphology of mouth parts reveals that they are similar in construction to other hermit crabs described earlier, but differ in details of setation. The chelipeds which are equal and similar are structurally well adapted for scooping and grasping and are effectively used both in sedimentary and particulate mode of feeding. The antennal flagella are not provided with plumose setae and are not used as filters for sieving suspended materials from the water column as reported already in 2 other hermit crabs.

In hermit crabs, information on feeding habits is available for *Pagurus prideauxi*[1], *Pagurus bernhardus*[2], *Diogenes brevirostris*[3], *Pagurus longicarpus*, *Pagurus pollicaris*[4] *Pagurus novae-zealandiae* and *Stratiotes setosus*[5]. All the above hermit crabs are largely bottom scavenging detritus feeders, however, in *D. brevirostris* and *S. setosus* the antennae are being used as an accessory feeding device for filtering plankton and this mode of feeding is called 'antennary cast net feeding'[3,5]. In species of *Pagurus* and in *S.setosus*, the chelipeds are unequal, the right chela being longer and bigger than the left one. In *D. brevirostris* the left chela is longer and bigger than the right. In these hermit crabs the chelipeds are not of much use in sedimentary feeding probably due to the unequal size of chela and the 3rd maxillipeds are used to pick up detritus directly. Information on the feeding behaviour of hermit crabs with equal chela is meagre and the role of the equal chelipeds is little understood. The present work was initiated to study the mouth parts of *Clibanarius longitarsus*, complete with setal types, to relate their structure and function and to elucidate the role of equal chelipeds during microphagy and macrophagy.

Materials and Methods

The mouth appendages were dissected from specimens preserved in 5% neutral formalin. Temporary glycerine mounts were used to verify certain details. Drawings of mouth parts and setal types were made with camera lucida. The stomach contents of few freshly collected animals were also examined under microscope. For behavioral observations the crabs were kept in cylindrical chambers. The substrate used for sedimentary type of feeding was collected from the place from where these animals were collected. For macrophagy, 2 types of food, the flesh of prawns and fish meal pellets were tried.

Results

Setal types—Microscopic examination of the whole mounts of mouth parts of this hermit crab revealed the following 6 types of setae.

Type 1 seta (Fig.1a): This can be separated into 2 portions by a faint transverse line suggesting the fracture plane. The proximal section is a nude cylinder. The distal portion tapers and is curved at its end. It bears 2 longitudinal rows of evenly spaced, distally directed fine, cuneate, setules. The setules are approximated at base.

Type 2 seta (Fig.1b): It is similar to type 1 in general outline, but is more robust. The setules are cuneate but are considerably bigger than those of type 1 setae. The setules are approximated at base just like in type 1 seta.

Type 3 seta (Fig. 1c): It is short and more robust than the above 2 types. It does not bear any setule and the margins are straight.

Type 4 seta (Fig.1d): Just like 3rd type of seta, this type is also robust with 2 diametrically opposed rows of larger setules. The setules are absent in the proximal and distal ends. Unlike the first 2 setae here the setules are irregular.

Type 5 seta: It is the plumose setae referred to by many authors. This is generally longer than other types, but shorter seta is also found in some appendages. The setules are fine hair attached in 2 diametrically opposed rows.

Type 6 seta: This is more variable with longest and shortest setae, either nude or with only a few randomly located, hair-like setules, may be hooked at the tip.

Description of mouth parts—The mouth parts of this hermit crab are placed one above the other. The inner mouth parts are closely positioned with the coxal endites posterior and closely situated to buccal opening. The 2nd maxillipeds, originating lateral to the 3rd maxillipeds are directed medially and their distal tips lie between proximal segments of 3rd

maxillipeds. The exopod of 3rd maxilliped is bigger than the 2nd maxilliped but they are held together and their flagella are directed medially. The exopod of 1st maxilliped is much shorter and directed towards the buccal opening.

Third maxilliped (Fig.1e): This is the most ventral mouth part with the bases approximated. It consists of 3 principal parts, coxa, exopod and endopod. The coxa bears types 5 and 6 setae along its lateral margins. The exopod has a long proximal segment bearing type 6 setae on both the outer and inner margins. The 2nd segment is tubular and short, about1/4 of the 1st segment and bears a few setae of type 6. Each segment of the many jointed flagellum is provided with 2 sets of type 5 setae on opposite sides forming 2 rows running the length of the flagellum.

The endopod consists of 5 segments. The 1st segment is the basi-ischium formed by the fusion of basis and ischium. The basi-ischium has a weakly developed denticulated ridge (the cresta dentata) running longitudinally which assists in grasping large food particles. The inner margin is beset with numerous setae of types 1 and 6. There are few setae of type 6 along its outer margin. The inner margin of merus and the distal portion of outer margin is beset with numerous setae of types 1 and 6 and there are few scattered setae of type 6 along the outer margin. The carpus has a thick brush of setae of types 1, 2 and 6 along the inner margin and a few scattered setae of type 6 along its outer margin. The setae on the inner margin overlap with those of the more distal segments when the limb is flexed. The propodus which is more or less equal to merus in length bears a few setae of types 1 and 6 along outer margin. There is a thick brush of setae at its distal end on the inner and outer sides which consists of setal types 1, 2 and 6. The dactylus is rounded at its distal end and is flattened dorsoventrally. On the dorsal surface there are numerous setae of types 3 and 4 intersped with each other. The inner margin is beset with a number of type 4 setae. There are also setae of types 1, 2 and 6 along its whole margin. The setae of propodus and dactylus overlap one another.

Second maxilliped (Fig.1f): This is located dorsal to the 3rd maxilliped and the bases are laterally situated. Just like the 3rd maxilliped it also consists of 3 principal parts, coxa, exopod and endopod, but they are smaller than the previous maxilliped. The setation of coxa and the proximal segment of exopod are the same as that of the previous maxilliped. The 2nd segment of exopod is tubular and bears type 6 setae at its distal end. The flagellar portion is also smaller than the previous type.

The endopod curves medially so that its tip lies between the proximal segments of the 3rd maxillipeds. It consists of 5 segments just like the previous type. But the dactylus is smaller than the previous type and in 3rd maxilliped, the merus and propodus are more or less equal in length, but here merus is the longest segment. The setation on the 1st two segments on the inner side is more or less the same as in the previous maxilliped, but there are no setae on the outer side. The carpus bears types 1 and 6 setae on the inner side and type 6 setae on the outer side. The propodus also bears types 1 and 6 setae. There is a brush of hair at the distal end of both inner and outer sides. The dactylus bears along its entire margin and also on its upper surface types 1, 2 and 6 setae. Just like in the previous maxilliped the setae of propodus and dactylus overlap one another.

First maxilliped (Fig.1g): In general outline it diverges sharply from the other maxillipeds and it resembles the maxillae with its coxal and basal endites. The coxal endite bears types 1 and 6 setae along its median border. The basal endite is spoon shaped with type 6 setae along its median border. The endopod is absent. The 1st segment of the exopod is more flattened and bears type 5 setae along its outer margin. The 2nd segment is considerably longer and bears a few type 6 setae. The flagellum bears type 5 setae in 2 rows as in other maxillipeds. Segmentation of the flagellum is incomplete.

Second maxilla (Fig.1h): The coxal and basal endites of this mouth part is unequally bilobed. The proximal lobe of coxal endite bears 3 rows of setae. The upper margin is beset with types 2 and 6 setae and the inner rows and lower margin are of type 5 setae. The distal lobe bears type 5 setae along its upper margin and bears type 6 setae along its inner margin. The endites of basis bear a thick mass of type 6 setae along its inner margin and also on the upper surface. The endopod which is a mere vestigial palp, is unsegmented and bears a few stiff type 6 setae. The exopod has been greatly modified to form the scaphognathite. The 1st segment has been flattened further than in the first maxilliped and a proximal lobe has been added, while the 2nd segment and flagellum are absent. The scaphognathite bears type 5 setae along its entire margin.

First maxilla (Fig.1j): Unlike the 2nd maxilla here the coxal and basal endites are single segmented and the whole appendage is very small. The coxal and basal endites are spoon shaped. The coxal endite bears type 6 setae along its inner margin and on its surface. The basal endite bears type 6 setae along its lateral margin and types 3 and 6 setae on its distal end. There is no exopod. The endopod is reduced to a palp, called the stipes. There are 2 spines on the dorsal knob-like

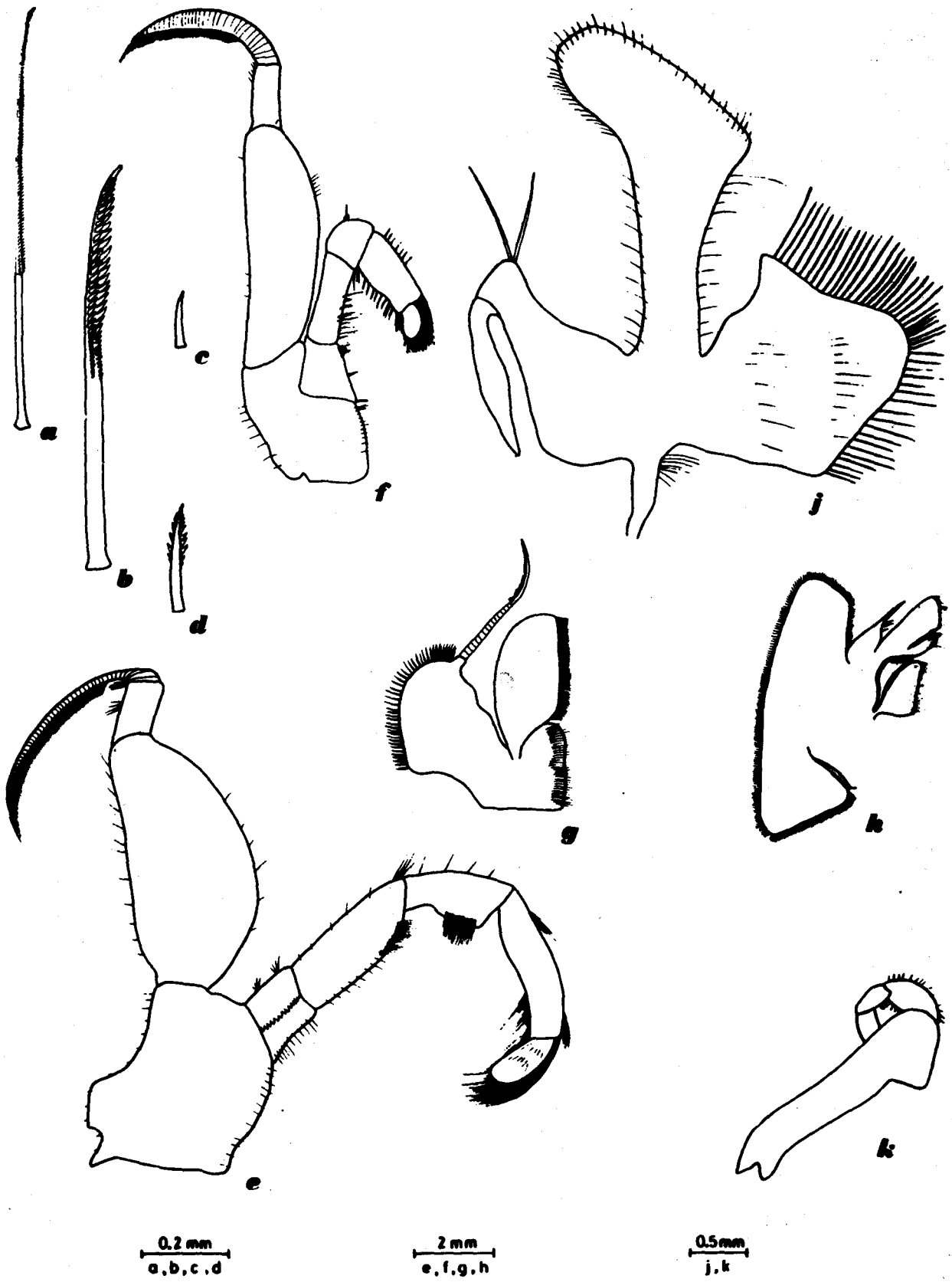

Fig. 1—Setal types and mouth parts of *C. longitarsus* (a-d, types 1-4 setae respectively; e, 3rd maxilliped; f, 2nd maxilliped; g, 1st maxilliped; h, 2nd maxilla; j, 1st maxilla and k, mandible)

portion. The lacina mobilis is considerably longer, but segments are not visible.

Mandible (Fig. 1k): The mandible is the only completely calcified mouth part. It is connected to the exoskeleton over much of its length and is well supplied with muscles. The lower side of both incisor and molar processes are provided with cutting edges. The palp arises proximal to the molar ridge on the anterior surface. This uncalcified structure consists of 3 segments so oriented that the terminal segment lies in the conspicuous groove formed by the molar and incisor processes. The terminal segment bears stiff, types 4 and 5 setae. The 2nd segment also bears a few type 5 setae.

Chelipeds: Eventhough the chelipeds are not mouth parts, as they aid in feeding, their structure is also to be mentioned here. The chelipeds are equal and similar in size and shape in this species. The inner side of both the fixed finger and dactylus are spoon shaped. This can be effectively used to pick up small particles and the picked up materials can be very well passed on to the 3rd maxilliped.

Feeding habits—C. longitarsus is largely a detritus feeder. Examination of the stomach contents showed that the bulk of the food consists of detritus, unidentifiable diatoms, algal filaments, crustacean remains and digested organic matter. In addition, the animals were also found to feed on muscles of gastropods, fishes and other animals.

Detritus feeding: In the laboratory, sedimentary feeding occurred even with the newly captured specimens. Surface layers of the bottom deposits containing sand grains and associated materials were scooped up by the chelipeds. The pereiopods were not involved in this mode of feeding. The 3rd maxillipeds subsequently held the sand grains and associated materials scooped by the chelipeds with the setae on the distal segments of endopod. These segments were alternately moved up and down and the sediment was brushed and transferred towards the inner mouth parts. Sorting of edible material from sand grain was accomplished by the third maxillipeds, maxillae and mandibles. Edible matter was separated from other materials by the spines and setae on the coxal and basal endites of the inner mouth parts. The materials to be ingested were positioned in front of the mouth opening. The materials to be discarded such as bigger sand grains, etc. were moved anteriorly and were thrown away by the fluttering action of exopods of 3rd and 2nd maxillipeds. Usually heavy materials thus discarded were thrown a few centimeters away from the animals. The fluttering of exopods were also noted to be intense when the animal was feeding on sediments. When more sediment was scooped, chelipeds and exopods of 3rd and 2nd maxillipeds on both sides worked actively. When the materials lifted were less the exopods fluttered alternately.

Feeding on large pieces of food—In nature: In the field, *C. longitarsus* was found to feed on many occasions on the flesh of dead gastropods. The local fishermen of Porto Novo bring in gastropods like *Hemifusus pugilinus* and *Rapana bulbosa* that are caught in trawlers. The opercula are of commercial value and after removing them they throw the animals into the estuary. The hermit crabs gather around them and feed on the flesh of these molluscs. In the fish landing area a variety of fishes and other animals are being thrown into the estuary and on these also the hermit carbs feed. The hermit carbs were observed to feed on cooked rice also when offered.

In Laboratory: Crabs captured from the field did not usually accept any food on that day but when starved in aquaria for a day or more after capture, accepted food more readily. Both the chelipeds were used to pick up larger particles. One cheliped was lifted and the animal rested on another cheliped and walking legs. The endopods of 3rd maxillipeds were lowered and the morsel was passed from the cheliped to 3rd maxilliped. If the food was passed immediately to the inner mouth parts, then the other cheliped was lifted and again the process was repeated. If the morsel was big, then one cheliped held the morsel and the other cheliped was used to tear off small bits of it and then this was passed on to maxillipeds.

The cresta dentata of the basi-ischium of 3rd maxilliped was used for holding the morsels. The 2nd maxilliped played a lesser role in holding the morsels. Further, manipulation of larger food tried in the present study varied. While the animal was feeding on flesh, from the maxilliped the flesh was pressed against the inner mouth parts. The 1st maxilliped, 2nd maxilla and 1st maxilla were drawn apart. The mandibles were also parted. The flesh was pushed between the mandibles by the 3rd maxilliped and the mandibles were brought together against it. The 3rd maxilliped then pulled the morsel downwards away from the mandible. This biting process was repeated until the whole flesh was swallowed.

While this animal was fed fish meal pellets, the 3rd maxillipeds held the pellets. The pellets were very delicate and not hard. The distal portion of 3rd maxilliped and the other inner mouth parts with their setae brushed the pellets and the small fragments thus freed were carried towards the mouth opening. Adhereing particles were passed anteriorly to the flagella.

Since food was abundant throughout the year in the field, the hermit crabs were not seen to eat their own kind. But in the laboratory when they were kept in starved condition for few days, it was not uncommon

to see some submissive animals being killed and their abdominal contents eaten by other animals.

In the laboratory the animals were also found to feed actively on algae that had grown along the walls of the glass trough. The algal filaments were scrapped by the chelipeds and passed on to the 3rd maxillipeds which inturn passed them to the inner mouth parts.

Relationship between morphology and function of mouth parts—The modification of mouth parts of the Paguridea from that of Brachyura is of functional significance[2] and the variations in structure of mouth parts of pagurid crabs were correlated with the differing functions[4]. The chelipeds of the paguridae need little discussion and they are structurally well adapted for scooping and grasping. In hermit crabs where the chelipeds are unequal, only the minor chela is used in sedimentary mode of feeding. In *C. longitarsus* where both the chelipeds are equal, they are effectively used both in particulate and sedimentary mode of feeding.

The 3rd maxilliped of pagurid crabs differs from that of true crabs where these structures are broadened to form an operculum over the inner mouth parts and an important function of the opercular maxillipeds in crabs is to retain food masses under pressure in contact with the cutting inner mouth parts so that the food can be readily and quickly subdivided and ingested. But in hermit crabs these are relatively unspecialized and do not form an operculum to the oral field. The weakly developed dentate ridge on the basi-ischium helps in grasping large food particles. The setal types 1, 2, 4, 5 and 6 present on the endites of *C. longitarsus* are useful in cleaning and combing. The density and the length of setae on the distal segments of endopod are suitable for holding small fragments of food and detritus which are to be passed on to the inner mouth parts.

The 2nd maxilliped, unlike the 3rd maxilliped, cannot hold large food particles. The setal types 1, 2 and 6 present on this appendage, are helpful in cleaning and feeding and they brush through the setae of 3rd maxillipeds and pass on the food particles to the inner mouth parts. The dense setae on the distal segments of endopod prevent food particles from being lost if dropped by the inner mouth parts. The exopods are similar to that of 3rd maxillipeds and are held together while the flagella beat and thus get rid of unwanted materials.

The dense rows of stiff setae on the endites of the 1st maxilliped, 2nd maxilla and 1st maxilla are associated with sorting edible materials from the sand grains and removing loose fragments from morsels. Setae present on the 2nd maxilla and 1st maxilla serve to present loosened material from escaping while providing no impediment to sand grains and large detrital material which is passed anteriorly by the movements of these limbs.

The mandibles are used for biting larger food particles. The setae of the mandibular palp are used to brush sand grains in conjunction with the setae of the maxillary endites.

The antenna of *C. longitarsus* is not provided with plumose setae and it cannot function as a filter in sieving suspended materials from the water column as noticed in *Diogenes brevirostris* and *Stratiotes setosus*[3, 5].

Discussion

C. longitarsus was found to be an omnivorous detritus feeder which utilizes food scrapped or sieved from the bottom deposits by the chelipeds and 3rd maxillipeds. Eventhough the mandibles are well developed, the weak development of cresta dentata on the 3rd maxilliped is associated with the reduced ability to grasp and tear large food objects between 3rd maxillipeds and mandibles. So scavenging and predation seem to be obligatory and opportunistic. The stomach contents examined also showed that the main source of food was bottom detritus.

Earlier works on the feeding behaviour of hermit crabs were done in animals with unequal chela. In *Pagurus bernhardus*[2] and *P. longicarpus*[4] where the right chela is more massive and longer than the left, only the minor chela aided in scooping detritus from the substratum and often the 3rd maxillipeds were used directly to scrap and catch various objects. In *Pagurus pollicaris* the chelipeds played no role in the transfer and the 3rd maxilliped directly picked up sand grains from the substratum[4]. The smaller left chela was most frequently used in *Pagurus novae-zealandiae* to lift bottom deposits to the mouth parts[5] In *Diogenes brevirostris* [3] and *Stratiotes setosus*[5] there is an auxillary method of feeding called as antennary cast net feeding where the suspended particles were filtered from the water column by the 2 rows of plumose setae on the antennae. But when there was little material in suspension the animal resorted to sedimentary mode of feeding. Here also only the minor chela was used to scoop sediments and the 3rd maxillipeds were often used directly to pick up materials from the substrate. *C. longitarsus* differs sharply from all the above hermit crabs in feeding behaviour. Probably due to the unequal size of chelae in all the above hermit crabs, only the minor chela was used to scoop sediments and on most instances the 3rd maxillipeds directly picked up food particles from the substratum. But in *C.longitarsus*, as both the chelipeds are of equal size and are small, they were effectively used both for

micro and macrophagy and the 3rd maxillipeds were not found to pick up food particles directly from the substratum. When the starved animals were allowed to feed on detritus, both the chelae worked efficiently and swiftly in the transfer of detritus to the 3rd maxillipeds. The loss of chelipeds in other hermit crabs was not a serious inpediment for feeding but in *C.longitarsus* the loss of chelipeds seriously affected feeding.

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