Zoomorphology

Functional Morphology of the Mouthparts and Associated Structures of *Pagurus rubricatus* (Crustacea: Decapoda: Anomura) with Special Reference to Feeding and Grooming

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Summary. *Pagurus rubricatus* is predatory, detrivorous, macrophagous, and to a small degree, a suspension feeder. The crab searches for small invertebrates by digging shallow pits in the sediment. During this process it feeds on detritus obtained either directly from the sediment or scoured off gravel granules. Particles trapped by the dense setation of the 2nd and 3rd maxillipeds are brushed off and ingested.

The distribution of the various types of setae on the mouthparts is mapped and structure of the mouthparts and their setae is correlated with function. Sediment collected by the pereiopods is brushed off by the endopodites of the 3rd maxillipeds and transferred to the inner mouthparts by the endopodites of the 2nd maxillipeds. The basipodites of the 1st maxillae form a filter screen through which particles of suitable size are pushed by the 2nd maxillae. Rejected particles are discarded by the exhalant stream via the currents generated by the exopodites of the maxillipeds. Specialized setae on the 2nd maxillae scour detritus from the surface of gravel granules applied to these appendages by the 2nd and 3rd maxillipeds. Interlocking setae from different appendages form a number of screens the main function of which is to retain material in the buccal region. The exopodite and endopodite of the 1st maxilliped and the endopodites of the 1st and 2nd maxillipeds form a channel which funnels the exhalant respiratory current away from the crab. The main grooming appendages are the endopodites of the 3rd maxillipeds, however, most of the other mouthparts have a self-cleaning function.

A. Introduction

Hermit crabs have classically been described as omnivorous scavengers or as detritus-feeders (Thompson 1904; Jackson 1913; Brock 1926; Orton 1927). More recent studies have shown, however, that members of this

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group employ a variety of feeding techniques including deposit-feeding, macrophagy, predation and suspension feeding (Boltt 1961; Roberts 1968; Greenwood 1972; Caine 1975, 1980; Gerlach et al. 1976; Schuhmacher 1977; Markham 1977; Kunze and Anderson 1979). While each species appears to have a preferred food source, most are able to feed in a number of ways and will switch from one feeding technique to another in order to exploit whatever food is readily available at the time (Kunze and Anderson 1979). This broad repertoire of feeding techniques in a single animal has led to an interest in the morphology of the feeding apparatus and in the adaptations for food gathering and processing.

Early purely morphological descriptions of hermit crab feeding structures have now been supplemented by studies on feeding behaviour and feeding adaptations in a number of species. However, few workers have attempted a functional analysis of the feeding structures. Greenwood (1972) has related differences in mouthpart setation between *Pagurus novaezelandiae* and *Stratiotes* (= *Paguristes*) *setosus* to differences in feeding habits. Caine (1975) in his study of the relationships between diet and feeding mechanism and gastric mill morphology in anomurans found some correlation between the morphology of the mouthparts and chelipeds and feeding activity for the four species of pagurids he studied. The most detailed study of hermit crab mouthpart functional morphology is that of Kunze and Anderson (1979). These authors studied four species of hermit crabs of the superfamily Coenobitoidea and for each described the structure of the mouthparts and proventriculus, mapped the distribution of the setae on the mouthparts and described feeding behaviour. They related structure to function and discussed their findings in the light of previous studies on feeding in hermit crabs.

As part of a study on the feeding adaptations of New Zealand hermit crabs, the functional morphology of the feeding structures of *Pagurus rubricatus*[1] was investigated.

P. rubricatus was found to be detrivorous, macrophagous, predatory and to a small extent a suspension feeder. Several important differences were found between this species and those studied by Kunze and Anderson (1979). In particular, *P. rubricatus* has a wider range of feeding mechanisms than any of the species studied by these authors, the setation of the mouthparts of *P. rubricatus* is more complex, the distribution of the setae is different and the mechanisms of handling, reduction and ingestion of the food and of particle selection also differ. One method of feeding used by *P. rubricatus* ('gravel-scrubbing') has not been previously described for hermit crabs.

This paper describes the feeding behaviour and morphology of the feeding and associated structures of *P. rubricatus* paying particular attention to the type and distribution of the setae. A functional analysis of the mouth-

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[1] The taxonomy of the New Zealand hermit crab fauna is currently under revision. *Pagurus rubricatus* (Henderson 1888) together with *P. spinulimanus* (Miers 1876) and the Miocene fossil *P. clifdenensis* Hyden and Forest 1980, will be transferred to a new genus (Hyden and Forest 1980)

parts and the role their setae play in feeding and the associated activities of grooming and generation of water currents is given, complementing and extending the observations of Kunze and Anderson (1979).

B. Material and Methods

Hermit crabs were collected by trawling off Otago Peninsula, South Island, New Zealand at depths of 60–90 m. The bottom in this region consists of gravels, sandy gravels and gravelly sands rich in organic skeletal debris (Andrews 1973; Probert et al. 1979). In the laboratory the crabs were kept on their natural substratum in holding tanks supplied with running seawater and fed at irregular intervals on polychaete worms and crushed bivalves.

For observation, individual crabs were placed in small (24 × 19 × 13 cm) 'Perspex' aquaria containing either mud, sand, gravel or the crabs' natural substratum. At least 5 crabs were observed on each substratum type. Gross observations of feeding behaviour were made in a darkroom using a 15 W red lamp as the only source of illumination. Detailed observations were made using a travelling stereomicroscope. Water currents were traced using suspensions of either fine mud particles or milk in seawater.

The gross morphology of the buccal apparatus was studied by dissection of animals narcotized in fresh water and then killed and fixed in 70% ethanol. Examination of partial dissections of the buccal region and animals cut in various planes, cleared in either glycerol or cedar wood oil and stained with haematoxylin proved useful in working out the relative arrangement of the appendages and their setation. Some 10 crabs were used for these detailed observations.

Individual mouthparts were dissected out, stained with lignin pink and examined under a stereomicroscope. Setae were studied using an SEM. For this selected structures were fixed in 70% ethanol, dehydrated, dried in a critical point drier, then mounted on aluminium stubs using colloidal graphite, coated with gold and examined in a Siemens Autoscan SEM.

C. Results

I. Feeding Behaviour

P. rubricatus is detrivorous and predatory. The crabs feed on sediment by excavating shallow trenches in the substratum using the minor (left) cheliped and the walking legs. The expanded outer edge of the propodite of the minor cheliped is dug into the sediment and the whole cheliped then pushed outwards away from the crab. The manus functions as a shovel pushing sediment in front of it (Fig. 1 A). At the same time, the dactyls of the 2nd and 3rd pereiopods scoop sediment in from the sides and kick it inwards underneath the shell and upwards towards the 3rd maxillipeds which collect it and transfer it to the other mouthparts (Fig. 1 A). Both pairs of walking legs are used and the usual sequence of events is: minor chela push, right 3rd pereiopod kick, right 2nd pereiopod kick, left 3rd pereiopod kick, minor chela push ... etc. The major (right) cheliped is rarely used to push away sediment. As the crabs dig, they move slowly backwards giving rise to characteristic trenches which may be up to 2 cm deep.

At intervals, the crabs stop digging and the minor chela is used to scoop up pincerfuls of sediment and transfer them to the mouthparts. The tip of the manus is planted firmly in the sediment and the whole cheliped is flexed such that sediment is collected on the concave ventral surface of the manus which is brought to lie underneath the 3rd maxillipeds (Fig. 1 B). The 3rd maxillipeds then transfer the sediment to the other
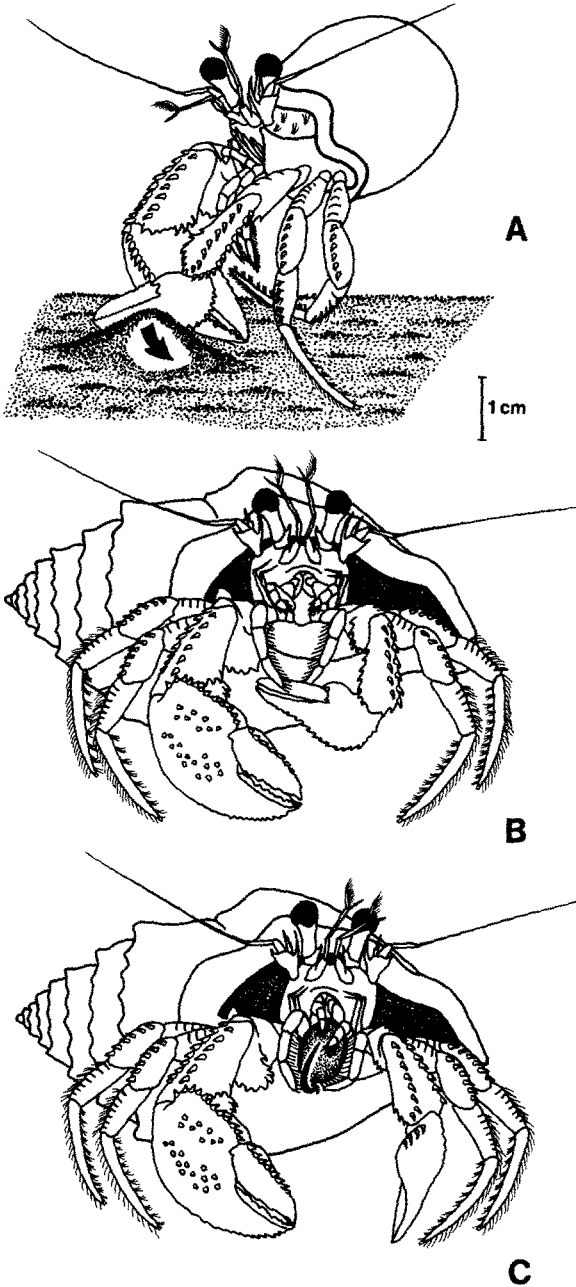
Fig. 1 A–C. Feeding behaviour of *Pagurus rubricatus*. A crab feeding on sediment. The minor chela pushes away surface sediment (*arrow*). The left 3rd pereiopod kicks sediment towards the 3rd maxillipeds. B crab brushing off detritus from the concave internal face of the minor chela using the 3rd maxillipeds. C 'gravel-scrubbing'. A gravel granule is cradled by the endopodites of the 2nd and 3rd maxillipeds while it is brushed by the inner mouthparts. The maxillipeds manipulate the granule and cause it to rotate in the direction shown by the arrow

mouthparts, the left 3rd maxilliped brushing particles from the ventral surface of the manus and the right 3rd maxilliped brushing the dorsal surface (Fig. 1 B).

Detritus is also obtained by a process best described as 'gravel-scrubbing'. Single pieces of gravel, shell fragments or other skeletal debris are picked out from the sediment by the minor chela and transferred to the mouthparts. The 2nd and 3rd maxillipeds manipulate the selected sediment granule and apply it against the inner mouthparts which perform vigorous brushing movements, after which the granule is discarded (Fig. 1 C). Pieces of skeletal material too large to be conveniently handled by the maxillipeds are crushed into smaller fragments by the major chela and each fragment is then scrubbed in turn.

Small gastropods and bivalves exposed during the digging activities of the crab are seized by the minor chela and cracked open by the major chela. The major chela is then used to hold the prey while the minor chela tears off pieces of flesh and transfers them to the mouthparts. Fragments of the cracked shells are transferred to the mouthparts and scrubbed in the same way as pieces of gravel.

When not foraging thus, *P. rubricatus* holds the densely setose endopodites of the 2nd and 3rd maxillipeds folded in front of the buccal region to form a screen. Beating of the exopodites of the maxillipeds creates a current of water which passes through this screen (Fig. 11). Particles carried in this current are trapped by the maxilliped setae and periodically brushed off and ingested.

II. Functional Morphology of the Buccal Structures

The structure of the mouthparts of *P. rubricatus* and the distribution of the various setal types on them are shown in Figs. 2–7. Different authors have used different nomenclatural schemes for decapod setae. The most widely used appears to be that of Thomas (1970) as modified by Factor (1978) and this is the scheme used here. In Figs. 2–7 setae intermediate between two of Factor's types are indicated by a slant line (e.g. E/G). Setae which have no equivalent in Factor's scheme are indicated by an asterisk (e.g. A*). To facilitate comparison between the present work and that of Kunze and Anderson (1979), the equivalent nomenclature of these authors' setal types 1–8 is given below:

Type 1–type I simple; type 2 = type F1 serrulate; types 3 and 4 are both variations of type D1 serrate setae; type 5 = type B2 pappose; type 6 = type A plumose; type 7 = type H1 cuspidate and type 8 are short type D1 serrate setae.

In the following descriptions, the *inner* surface of an appendage is that facing the mouth while the *outer* surface is that opposite. The terms *medial* and *lateral* are used in a morphological sense to distinguish between the two edges of an appendage when straightened. The *medial* edge is that nearest the midline of the body and the *lateral* edge is that opposite. *Upward*
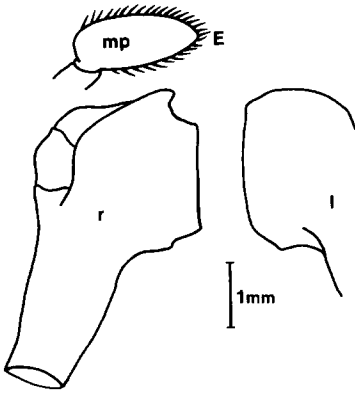
Fig. 2. *Pagurus rubricatus*. Mandibles and right mandibular palp (inset) in external view. *l*, left mandible; *mp*, mandibular palp; *r*, right mandible. The remaining symbol refers to the setal nomenclature scheme of Factor (1978) (see text)
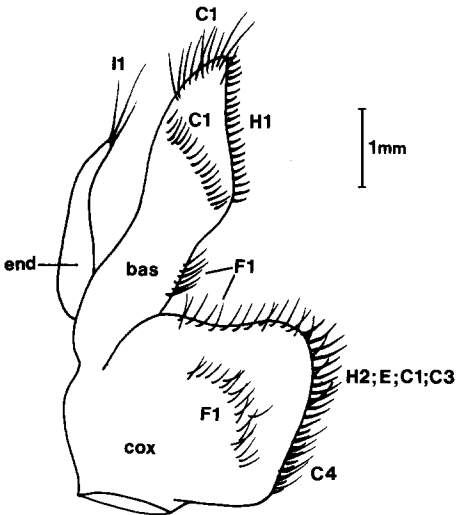

Fig. 3. *Pagurus rubricatus*. Right 1st maxilla in external view. *bas*, basipodite; *cox*, coxopodite; *end*, endopodite. The remaining symbols refer to the setal nomenclature scheme of Factor (1978)

and *downward* movements refer to movements in the direction of the tip and the base of the mouthpart respectively.

III. Feeding

The mouthparts and other associated structures together with their setal complexes form a number of functionally discrete structural units which divide the space in front of the mouth into three regions here termed the posterior, mid and anterior buccal spaces.

The posterior buccal space lies immediately in front of the mouth and is delimited by the labrum and mandibular palps dorsally, by the molar process, palp and incisor process of the mandibles laterally and by the bodywall, paragnaths and setae of the ventral mid-buccal screen (see below) ventrally (Fig. 8). During feeding the mandibles are normally held slightly apart giving free access to the mouth. On the distal segment of the mandibular palps are numerous rows of type E triserrate setae which point towards its tip (Fig. 2). When feeding on fine material the two mandibular palps

Fig. 4. *Pagurus rubricatus.* Right 2nd maxilla in external view. *bas,* basipodite; *cox,* coxopodite; *end,* endopodite; *scaph,* scaphognathite. The remaining symbols refer to the setal nomenclature scheme of Factor (1978). Setal fields on the internal face of the appendage are indicated by broken arrows. For the medial edge setae the outer, middle and inner setal fields are labelled (*a*), (*b*) and (*c*). respectively
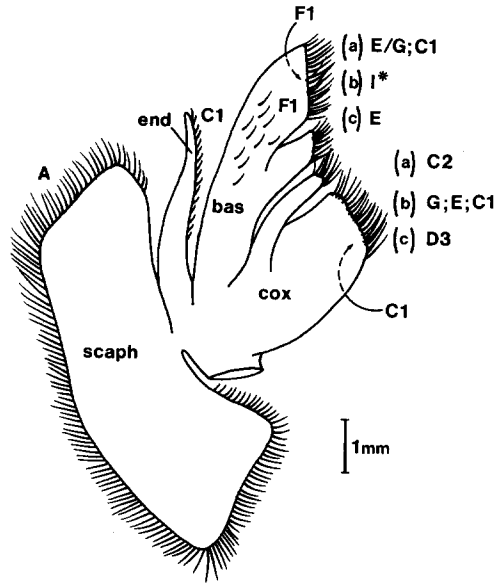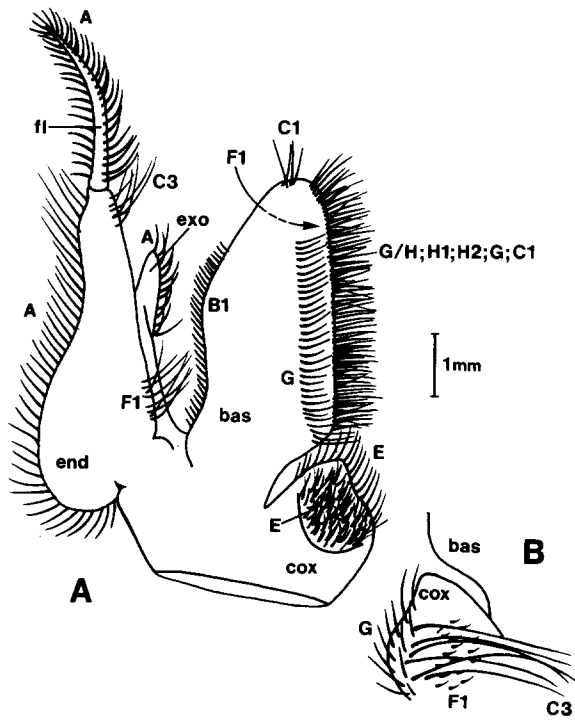
Fig. 5A, B. *Pagurus rubricatus.* A Right 1st maxilliped in external view. B Coxopodite of right 1st maxilliped in internal view. *bas,* basipodite; *cox,* coxopodite; *end,* endopodite; *exo,* exopodite; *fl,* flagellum. The remaining symbols refer to the setal nomenclature scheme of Factor (1978). The broken arrow indicates a setal field on the internal face of the appendage

are applied against each other such that the fields of setae on their morphologically lateral edges intermesh to form a screen which prevents particles from escaping dorsally from the posterior buccal space (Fig. 9). During biting the palps together with the labrum hold the food steady while the mandibles slice through it.

    The mid-buccal space is delimited by the 1st and 2nd maxillae the basipo-
dites and coxopodites of which form two functionally distinct units (Fig. 8).
Each basipodite of the 1st maxillae bears four rows of type Hl cuspidate
setae on its medial edge (Fig. 12 A). The outermost row consists of stout,
widely spaced setae which point medially. Staggered behind these is a double
row of more slender setae which also point medially. Behind this double
row is a single row of setae which point slightly backwards and arranged
in such a way that each inner row seta is approximately in line with an
outer row seta (Fig. 12 A). When the left and right basipodites of the 1st
maxillae are applied against each other these rows of cuspidate setae form
a grating in front of the mouth (Figs. 8 and 9), which serves as a filter.
    Particles are pushed through the grating by the basipodites of the 2nd
maxillae. Subterminally along their inner faces these bear a row of type E
triserrate setae (Fig. 4), which curve backwards and intermesh with the grat-
ing setae of the 1st maxillae (Figs. 8 and 9). With each stroke of the 2nd
maxillae, these triserrate setae push material through the grating and into
the mouth. Because the triserrate setae point slightly upwards, particles
too large to pass through the grating are progressively pushed upwards
until they are discarded via the rejection current. The triserrate setae of
the basipodites of the 2nd maxillae have the additional function of abrading
the food during macrophagous feeding.
    Medially the basipodites of the 2nd maxillae bear numerous rows of
specialized simple setae (I* setae) which have recurved and slightly flattened
tips (Fig. 12 B). These are reminiscent of the spoon-tipped setae of ocypodid
crabs (Miller 1961) and have the similar function of scouring off detritus
from the surface of large granules during 'gravel-scrubbing'. Subterminally
along the outer medial edge of the basipodites there is a row of forward
pointing setae which are intermediate between type G triserrulate and type E
triserrate (Fig. 4). These have the double function of forming a screen be-
tween the basipodites of the 2nd maxillae and those of the 1st maxilliped
(Fig. 9) and of abrading soft material as the 2nd maxillae beat.
    Fields of setae on the coxopodites of the 1st and 2nd maxillae intermesh
with each other and with very long backwardly directed setae from the
coxopodite of the 1st maxilliped to form the floor of the mid-buccal space
and continue backwards through the gap between the mandibles to form
part of the floor of the posterior buccal space (Fig. 8). The coxopodites
of the 1st maxillae are flattened flap-like structures which curve orally
(Fig. 3). Along their medial edges these carry a mixture of long type H2
cuspidate and type E triserrate setae and shorter type C1 and C3 plumoden-
ticulate setae. More ventrally type C4 plumodenticulate setae predominate
(Fig. 3). All these setae intermesh with those of the opposite appendage
and with setae from the coxopodites of the 2nd maxillae. The longest setae
also intermesh with the very long type C3 plumodenticulate setae of the
coxopodites of the 1st maxillipeds and pass backwards into the posterior
buccal space (Fig. 8). Type Fl serrulate setae on that edge of the coxopodite
just beneath the head of the basipodite intermesh with similar setae on
the neck of the basipodite to fill the gap between these two segments (Fig. 3).

On their medial edges the coxopodites of the 2nd maxillae bear two rows of setae. The outer row consists mainly of type G triserrulate setae with a few type E triserrate and type C1 plumodenticulate setae (Fig. 4). These setae point medially and intermesh with those of the opposite append-age. The inner row consists of type D3 serrate setae which curve backwards and intermesh with the medial edge setae of the coxopodites of the 1st maxillae and with the very long setae of the coxopodite of the 1st maxilliped (Figs. 4 and 8). This complex of intermeshing setae forms a screen beneath the basipodites of the 1st and 2nd maxillae and prevents particles from falling out ventrally from the mid-buccal space (Fig. 8).

The 1st, 2nd and 3rd maxillipeds delimit the anterior buccal space which, like the mid-buccal space, may be divided into functionally distinct dorsal and ventral regions (Fig. 8). The basipodites of the 1st maxillipeds are door-like structures which bear fields of setae along their medial edges (Fig. 5). These setae consist of long type H1 and H2 cuspidate, type G triserrulate and types intermediate between the two. Interspersed amongst these are shorter type G triserrulate and type C1 plumodenticulate setae. All these setae curve towards the mouth and intermesh with the corresponding setae of the opposite basipodite to form a setal screen which separates the anterior buccal space from the mid-buccal space (Fig. 9). The curvature of the screen setae and the arrangement of their setules is such that material may pass through the screen in the direction of the mouth but not in the reverse direction.

The fingers (i.e. the dactyl, propodite and carpopodite) of the 2nd and 3rd maxillipeds have analogous functions during feeding. Those of the 3rd maxillipeds transfer material from the chelae and walking legs to the anterior buccal space while those of the 2nd maxillipeds push this material posteriorly into the mid-buccal space through the screen separating these two regions. In addition, during 'gravel-scrubbing' or macrophagous feeding the fingers of the 2nd and 3rd maxillipeds firmly press the food or sediment granule against the inner mouthparts (Fig. 1C).

The propodite and dactyl of the 2nd maxillipeds bear fields of serrate and serrulate setae along their morphologically medial edges and on their inner faces (Figs. 6A and B). These setae are used as combs to brush material from the fingers of the 3rd maxillipeds. When the endopodites of the 2nd maxillipeds are folded, the setae on the morphologically medial edges of the dactyl and propodite intermesh with those of the opposite segments; the long type G triserrulate setae situated dorsally on the morphologically lateral edge of the propodite intermesh with the corresponding setae of the opposite propodite. The two fingers thus form a roof to the anterior buccal space (Fig. 8). The long cuspidate setae of the dactyls are used to grip the food during macrophagous feeding.

The fingers of the 3rd maxillipeds have fields of serrate, serrulate and plumodenticulate setae of a variety of types along both edges of the dactyl, on the morphologically medial edges of the propodite and carpopodite, and on the inner faces of all three segments (Figs. 7A and B). These setae function in scraping material from the pereiopods and transferring it to
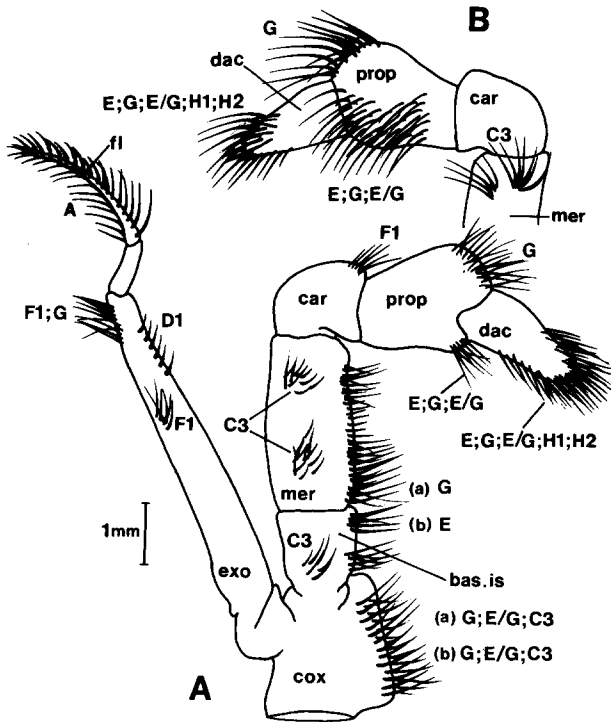
Fig. 6 A, B. *Pagurus rubricatus*. A Right 2nd maxilliped in external view. B Finger of right 2nd maxilliped in internal view. *bas.is*, basi-ischiopodite; *car*, carpopodite; *cox*, coxopodite; *dac*, dactylopodite; *exo*, exopodite; *fl*, flagellum; *mer*, meropodite; *prop*, propodite. The remaining symbols refer to the setal nomenclature scheme of Factor (1978). For the medial edge setae the outer and inner setal fields are labelled (*a*) and (*b*) respectively
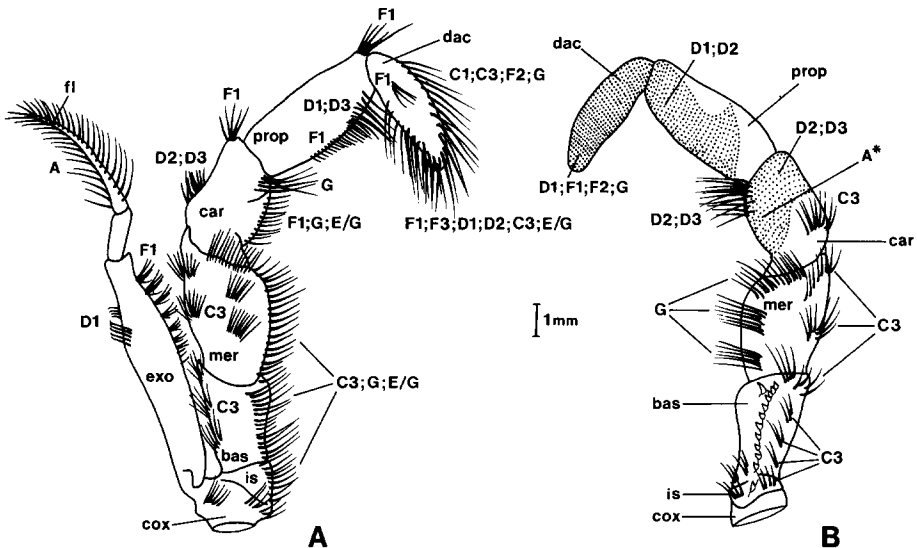

Fig. 7 A, B. *Pagurus rubricatus*. A Right 3rd maxilliped in external view. B Endopodite of right 3rd maxilliped in internal view. *bas*, basipodite; *car*, carpopodite; *cox*, coxopodite; *dac*, dactylopodite; *exo*, exopodite; *fl*, flagellum; *is*, ischiopodite; *mer*, meropodite; *prop*, propodite. The remaining symbols refer to the setal nomenclature scheme of Factor (1978). In B setal insertions on the finger are indicated by dots
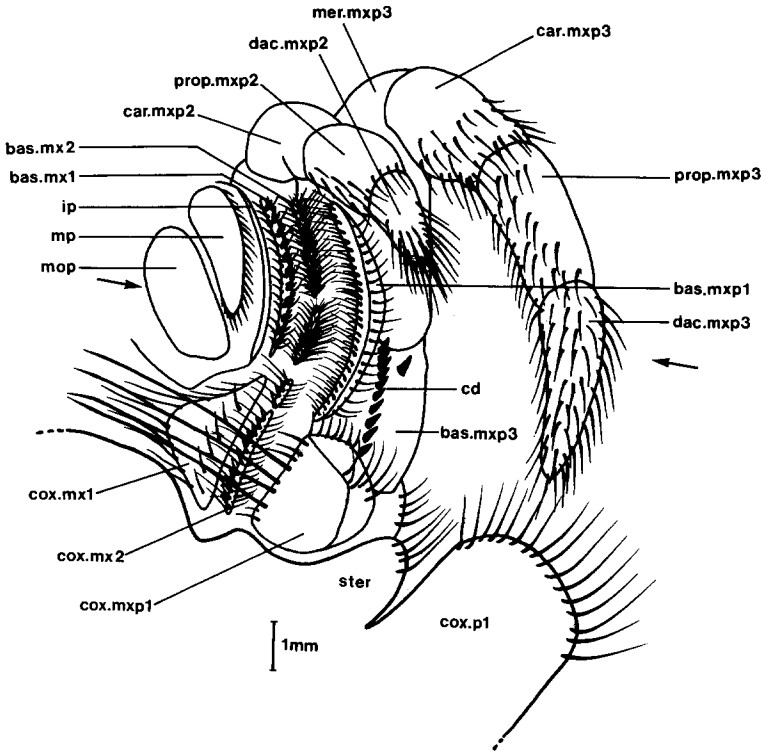
Fig. 8. Sagittal section through the buccal region of *Pagurus rubricatus* showing the relative arrangement of the mouthparts of the left side. For clarity fewer setae than actually present are shown. *bas.mx1*, basipodite of the 1st maxilla; *bas.mx2*, basipodite of the 2nd maxilla; *bas.mxp1*, basipodite of the 1st maxilliped; *bas.mxp3*, basipodite of the 3rd maxilliped; *car.mxp2*, carpopodite of the 2nd maxilliped, *car.mxp3*, carpopodite of the 3rd maxilliped; *cd*, crista dentata; *cox.mx1*, coxopodite of the 1st maxilla; *cox.mx2*, coxopodite of the 2nd maxilla; *cox.mxp1*, coxopodite of the 1st maxilliped; *cox.p1.* coxopodite of the cheliped; *dac.mxp2*, dactylopodite of the 2nd maxilliped; *dac.mxp3*, dactylopodite of the 3rd maxilliped; *ip*, incisor process; *mer.mxp3*, meropodite of the 3rd maxilliped; *mop*, molar process; *mp*, mandibular palp; *prop.mxp2*, propodite of the 2nd maxilliped; *prop.mxp3*, propodite of the 3rd maxilliped; *ster*, 8th thoracic stermite

the other mouthparts (Fig. 1 B). When the endopodites are folded, the fingers of the 3rd maxillipeds come to lie under those of the 2nd maxillipeds and between the coxopodites of the chelipeds. The fields of setae on the inner faces of the fingers intermesh with those of the opposite appendage while long setae at the tips of the dactyls intermesh with upward pointing setae from the medial edges of the coxopodites of the chelipeds to form the outer wall of the anterior buccal space (Fig. 8).

Ventrally, the anterior buccal space is delimited by the coxopodites of the 1st, 2nd and 3rd maxillipeds. Setae from these segments and from the 8th sternite (i.e. that bearing the 3rd maxillipeds) intermesh to form a floor to the anterior buccal space (Fig. 8). The coxopodites of the 1st maxillipeds are shaped like truncated cones (Fig. 5A). On their medial surfaces there
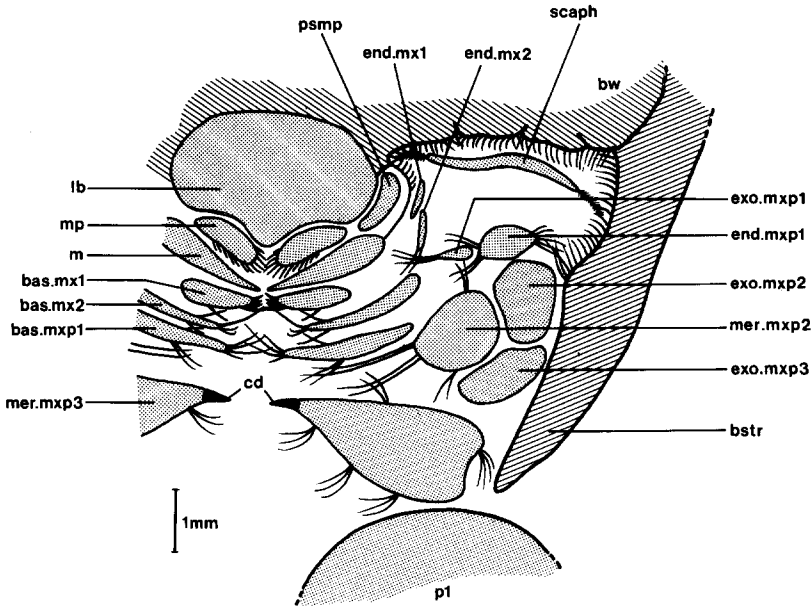
Fig. 9. Transverse section through the buccal region of *Pagurus rubricatus* in the plane indicated by the arrows in Fig. 8. *bas.mx1*, basipodite of the 1st maxilla; *bas.mx2*, basipodite of the 2nd maxilla; *bas.mxp1*, basipodite of the 1st maxilliped; *bstr*, branchiostegite; *bw*, body wall; *cd*, crista dentata; *end. mx1*, endopodite of the 1st maxilla; *end.mx2*, endopodite of the 2nd maxilla; *end.mxp1*, endopodite of the 1st maxilliped; *exo.mxp1*, exopodite of the 1st maxilliped; *exo.mxp2*, exopodite of the 2nd maxilliped; *exo.mxp3*, exopodite of the 3rd maxilliped; *lb*, labrum; *m*, mandible; *mer.mxp2*, meropodite of the 2nd maxilliped; *mer.mxp3*, meropodite of the 3rd maxilliped; *mp*, mandibular palp; *p1*, cheliped; *psmp*, proximal segment of mandibular palp; *scaph*, scaphognathite

is a field of setae of two types (Fig. 5 B). One type are long slender type G triserrulate which point towards and intermesh with the corresponding setae of the opposite segment and serve to lock the two coxopodites together. The other type are very long type C3 plumodenticulate which curve orally and continue past the coxopodites of the two maxillae and past the mandible to pass into the mouth (see above and Fig. 8). Along the posterior edge of the upper (truncated) surface, the coxopodites bear fields of upward pointing type E triserrate setae which lie underneath the basipodites of the 1st maxillipeds and intermesh with their proximal medial edge setae (Fig. 5A). On the anterior edges of the coxopodites there is another field of type E triserrate setae (Fig. 12C) which point anteriorly and curve medially (Fig. 5A). These setae intermesh with similar setae from the middle region of the 8th sternite and with triserrulate and plumodenticulate setae from the medial edges of the coxopodites of the 2nd and 3rd maxillipeds to form the floor of the anterior buccal space (Fig. 8).

In addition to the setae already described, most of the buccal appendages possess two further groups of setae, one situated on the outer face and pointing anteriorly and the other on the inner face and pointing posteriorly (Figs. 3–7). The anteriorly pointing setae on the outer face of one appendage

intermesh with the posteriorly pointing setae on the inner face of the adjacent appendage to form a lateral screen between the two appendages which prevents material from falling out laterally from the buccal spaces (Fig. 9). Thus, type C1 plumodenticulate setae on the outer face of the basipodite of the 1st maxilla intermesh with type F1 serrulate setae on the inner face of the 2nd maxilla; setae intermediate between types G and E on the outer face of the basipodite of the 2nd maxilla intermesh with type F1 serrulate setae on the inner face of the basipodite of the 1st maxilliped and type G triserrulate setae on the outer face of the basipodite of the 1st maxilliped intermesh with type E triserrate setae on the meropodite of the 2nd maxilliped (Fig. 9). Similarly, type F1 serrulate setae on the outer face of the coxopodite of the 1st maxilla intermesh with type C1 plumodenticulate setae on the inner face of the 2nd maxilla and type C2 plumodenticulate setae on the outer face of the coxopodite of the 2nd maxilla intermesh with type F1 serrulate setae on the inner face of the coxopodite of the 1st maxilliped.

When the endopodites of the 2nd and 3rd maxillipeds are folded underneath the other mouthparts, type G triserrulate setae on the medial edges of the meropodite and triserrulate, triserrate and plumodenticulate setae from the medial edges of the basi-ischiopodite of the 2nd maxilliped intermesh with backward pointing triserrulate, triserrate and plumodenticulate setae on the medial edges of the meropodite and basi-ischiopodite of the 3rd maxilliped to form a lateral screen between these two appendages (Fig. 9). This screen is also the lateral wall of the anterior buccal space.

IV. Grooming

The main grooming appendages are the 3rd maxillipeds although most of the other mouthparts have a self-grooming function. The majority of the mouthpart setae, particularly those making up the various screens, are covered with setules which often have serrated edges. Particles adhering to the setae are detached by the setules as the setae slide over each other during the normal movements of the mouthparts. Because of the orientation of the setules about the shaft, these detached particles can only move towards the tip of the seta and are progressively carried distally until they are either ingested or rejected.

The 3rd maxillipeds are responsible for cleaning the eyes, antennae, antennules, chelipeds, walking legs and anterior part of the carapace. In the case of the eyes, antennules and antennae, the base of the appendage is grasped from either side by the dactyls and propodites of the 3rd maxillipeds which are then drawn distally towards the tip of the appendage which at the same time is pulled in the opposite direction. The aesthatasc setae of the antennule are cleaned by special type D2 and D3 serrate setae situated medially on the distal portion of the carpopodites of the 3rd maxillipeds (Fig. 7B). The two carpopodites are brought together one on either side of the antennular flagellum and the aesthatasc setae are then drawn through these fields of cleaning setae. The inner face of the carpopodites of the
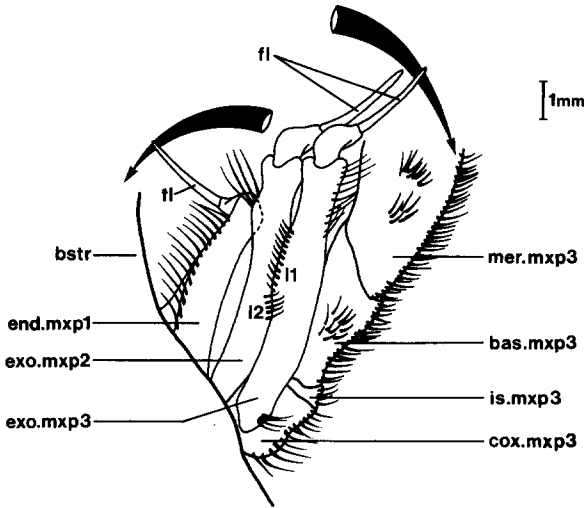
Fig. 10. Lateral view of the buccal region of *Pagurus rubricatus* showing the relative arrangement of the endopodite of the 1st maxilliped and the exopodites of the 2nd and 3rd maxillipeds of the right side and the paths traced by their flagella. For clarity the flagellar setae are not shown. *bas.mxp3*, basipodite of the 3rd maxilliped; *bstr*, branchiostegite; *cox.mxp3*, coxopodite of the 3rd maxilliped; *end.mxp1*, endopodite of the 1st maxilliped; *exo.mxp2*, exopodite of the 2nd maxilliped; *exo.mxp3*, exopodite of the 3rd maxilliped; *fl*, flagella; *is.mxp3*, ischiopodite of the 3rd maxilliped; *l1*, latching setae of the exopodite of the 3rd maxilliped; *l2*, latching setae of the exopodite of the 2nd maxilliped; *mer.mxp3*, meropodite of the 3rd maxilliped

3rd maxillipeds has an additional type of cleaning setae (A* setae; Fig. 7 B). These resemble type A plumose setae except that they bear short, serrated setules instead of long filamentous ones (Fig. 12 D).

The pincer of the chelipeds is held vertically between the 2nd and 3rd maxillipeds. Using the setae on the medial edges of the fingers, these then brush the pincer – the left pair of appendages brushing one surface while the right pair brush the opposite surface. The two 2nd maxillipeds work the distal half of the pincer starting from the base of the dactyl and brushing towards the tip while the two 3rd maxillipeds work the proximal half. The remainder of the chelipeds, the walking legs and the anterior part of the carapace are brushed by the setae of the inner faces of the 3rd maxillipeds. The 2nd and 3rd maxillipeds clean themselves by rubbing against the opposite appendage.

V. Rejection Currents

Particles are discarded via the strong exhalant current from the branchial chambers. This current is generated by the beating of the scaphognathites of the 2nd maxillae in a manner similar to that described for other decapods. As in other decapods, the edges of the scaphognathite are lined with type A plumose setae (Fig. 4) which serve both to extend its surface area and act as a gasket.

The posterior wall of the exhalant channel is formed by the body wall while posterolaterally it is formed by the branchiostegite (Fig. 9). The exopo-

Fig. 11. Anterolateral view of *Pagurus rubricatus* showing water currents generated by beating of the exopodites of the right 2nd and 3rd maxillipeds. For clarity the right cheliped has been cut (*shaded*). A, anterolateral current from left side of body; B, lateral and C, ventrolateral currents from right side of body; D, current from surface of substratum; E, medial current. The exhalant current emerges at right angles to the plane of the paper at the point marked *X*. Note position of the antennules
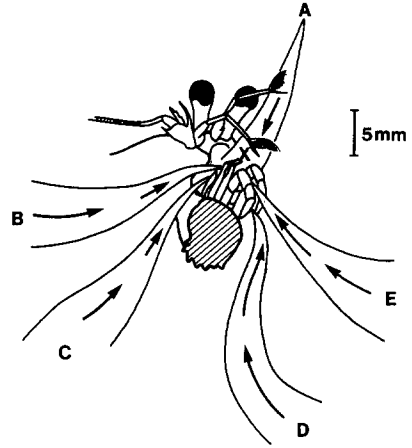
dite of the 1st maxilliped slots against the medial edge of the endopodite of the same appendage such that these two segments form a single structure (Fig. 5A). Along its lateral edge the endopodite carries type A plumose setae which intermesh with other setae lining the internal surface of the branchiostegite (Fig. 9). Setae lining the medial edge of the endopodite intermesh with backward pointing setae from the inner face of the meropodite of the 2nd maxilliped. Type A plumose setae lining the medial edge of the exopodite of the 1st maxilliped intermesh with type C1 plumodenticulate setae lining the endopodite of the 2nd maxilla (Fig. 9). These plumodenticulate setae also bridge the gap between the endopodite and the lateral edge of the basipodite of the 2nd maxilla. The endopodite of the 1st maxilla slots against that of the 2nd maxilla and against the bodywall. Thus the exopodite and endopodite of the 1st maxilliped and the endopodites of the 1st and 2nd maxillae lock together by means of setae and bevelled surfaces to form the anterior and anterolateral walls of the exhalant channel (Fig. 9). This channel serves to funnel water upwards and anterolaterally away from the crab (Fig. 11).

The flagella of the exopodites of the 2nd and 3rd maxillipeds generate currents which waft water from the substratum surface immediately in front of the crab up between the chelipeds and endopodites of the 3rd maxillipeds and into the exhalant stream. Water is also drawn into the exhalant stream from the sides of the crab (Fig. 11). Normally, either the left or the right exopodites beat at any one time. The antennule on the same side as the beating exopodites dips down and samples the water current coming up from the substratum surface while the other antennule is held erect and samples the water coming in obliquely from the side (Fig. 11).

The exopodites of the 2nd and 3rd maxillipeds lie adjacent to each other and are arranged parallel to the long axis of the body (Figs. 9 and 10). The exopodite of the 3rd maxilliped carries two rows of type D1 serrate setae (Fig. 7A) which wrap round the exopodite of the 2nd maxilliped and latch on to appropriately arranged fields of serrulate and serrate setae on this appendage (Fig. 10). In turn, type F1 serrulate setae from the exopodite

of the 2nd maxilliped (Fig. 6A) grip the edge of the exopodite of the 3rd maxilliped (Fig. 10). The two exopodites are thus locked firmly together and function as one unit, the flagella of the two exopodites beating together in a frontal plane and describing a small arc (Fig. 10). Type F1 serrulate setae on the medial edge of the exopodite of the 3rd maxilliped intermesh with fields of type C3 plumodenticulate setae on the lateral edges of the meropodite of the 3rd maxilliped to form a screen between the exopodite and endopodite of this appendage (Fig. 7A).

The long axis of the endopodite of the 1st maxilliped is inclined at a small angle relative to the long axes of the exopodites of the 2nd and 3rd maxillipeds, and, being shorter, its flagellum lies below the flagella of the two exopodites (Fig. 10). The flagellum of the 1st maxilliped beats in synchrony with the flagella of the 2nd and 3rd maxillipeds but is arranged such that it generates a current which wafts particles up from the dorsal region of the mid-buccal space and into the currents generated by the exopodites of the 2nd and 3rd maxillipeds and, via these, into the exhalant stream. At the lowest point of its stroke the flagellum of the 1st maxilliped comes to lie across a tuft of long type C3 plumodenticulate setae carried distally on the inner face of the meropodite of the 2nd maxilliped (Figs. 6B and 12E). The exact function of these setae is not clear but they appear to act as a buffer for the flagellum and may also serve to detach particles trapped in its setae.

Along their edges the flagella of the maxillipeds bear type A plumose setae (Figs. 5A, 6A, 7A). Each flagellum beats dorsoventrally (Fig. 10). As the flagellum moves dorsally (upstroke), water resistance acts on the plumose setae and causes them to spread. As the flagellum moves ventrally (downstroke), the setae are folded. The upstroke is thus the power stroke while the downstroke is the recovery stroke. A ventral projection at the base of each plumose seta just above the point of articulation catches on a ledge associated with each setal insertion when the setae are fully spread and prevents them from folding during the upstroke (Fig. 12F).

VI. Mouthpart Function During Feeding

1. Detritus Feeding. Working alternately the 3rd maxillipeds collect sediment from the pereiopods using the setae of the dactyls and propodites (Fig. 1A). The fingers of the 3rd maxillipeds are then flexed medially such that the

Fig. 12. A Type H1 cuspidate setae of the medial edge of the basipodite of the 1st maxilla. These setae form a sieve screen in front of the mouth. Outer face of the basipodite is at right (× 70). **B** Modified simple setae from the medial edge of the basipodite of the 2nd maxillae (I* 'gravel-scrubbing' setae, Fig. 4). Note recurved and slightly flattened tips (× 400). **C** Type E triserrate setae from the outer face of the coxopodite of the 1st maxilliped (Fig. 5A) (× 220). **D** Modified plumose setae from the inner face of the carpopodite of the 3rd maxillipeds (A* setae, Fig. 7B) (× 140). **E** Long type C3 plumodenticulate setae from the internal face of the meropodite of the 2nd maxilliped (Fig. 6B). These setae act as a buffer for the flagellum of the 1st maxilliped (× 210). **F** The basal region of type A plumose setae from the flagellum of the 2nd maxilliped. Note the projection at the base of each shaft (arrows) and the groove associated with each setal insertion (× 500)
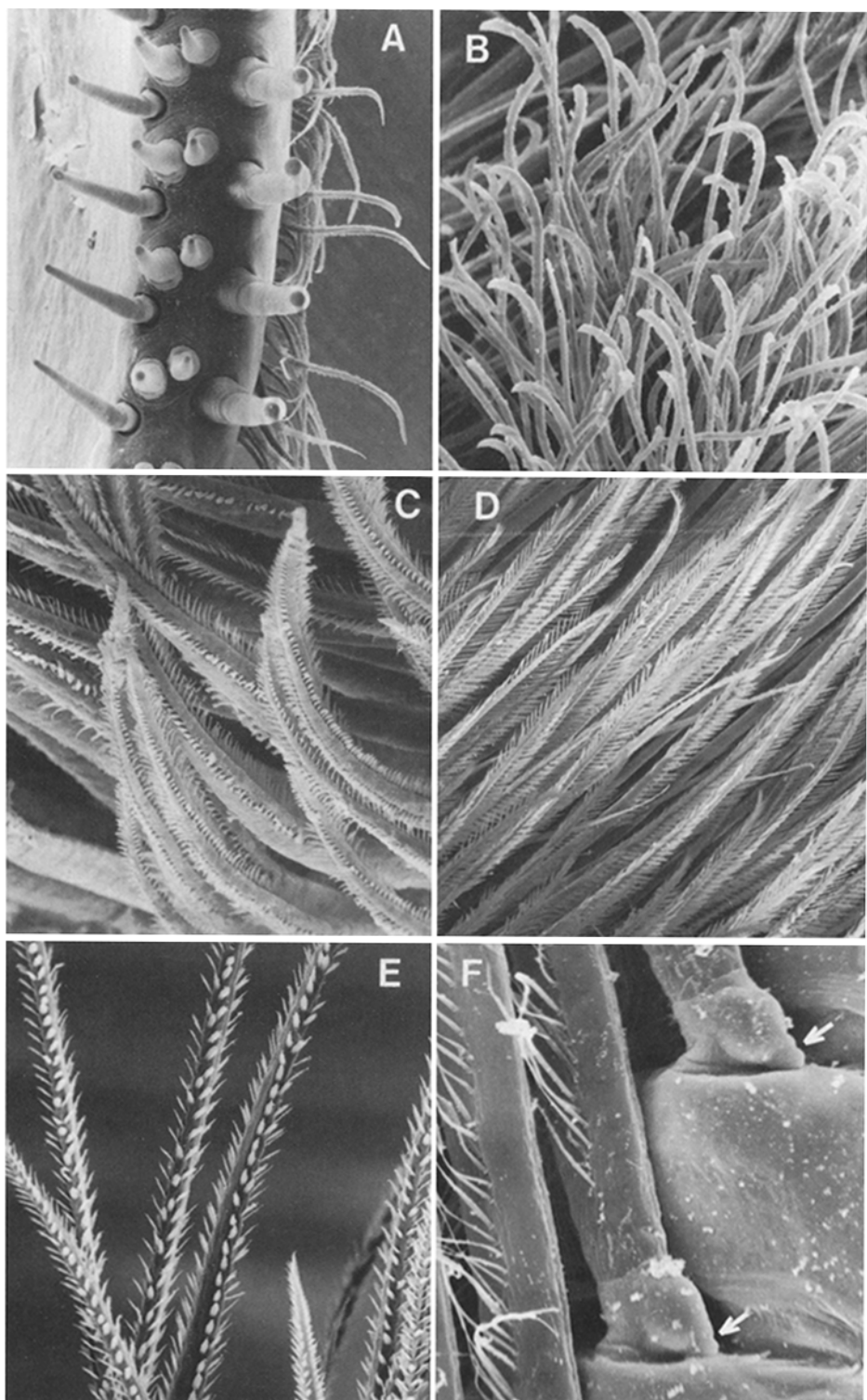
distal segments come to lie underneath the other mouthparts (Fig. 1 B). Also working alternately the dactyls of the 2nd maxillipeds rake off particles from the setae of the fingers of the 3rd maxillipeds and push them through the setal screen formed by the basipodites of the 1st maxillipeds and into the mid-buccal space. Here the vigorous mediolateral beats of the basipodites of the 2nd maxillae tease off particles from the dactyl setae of the 2nd maxilliped. The basipodites of the 1st maxillipeds also perform a small mediolateral movement which helps to dislodge particles adhering to the distal segments of the 2nd maxillipeds and to push them posteriorly into the mid-buccal space. Propelled by the 2nd maxillae fine particles are pushed backwards through the filter screen formed by the medial edge setae of the basipodites of the 1st maxillae; larger inorganic particles are pushed upwards towards the distal tips of the maxillae where they are carried away by the rejection currents. Throughout this process the basipodites of the 1st maxillae remains static or at most perform a very low amplitude mediolateral vibration. The mandibles, mandibular palps and the labrum similarly remain static. If however live foraminifera were present, these were passed into the posterior buccal space where they were cracked open by the molar processes of the mandibles. The mandibular palps then pushed out the resulting fragments into the mid-buccal space where they were treated as other detrital particles.

2. Gravel-scrubbing. Granules of suitable size are grasped by the endopodites of the 2nd and 3rd maxillipeds which hold them applied against the inner mouthparts (Fig. 1 C). The basipodites of the 1st maxillipeds and of the 2nd maxillae perform energetic mediolateral movements, those of the 2nd maxillae being especially vigorous, and scour off detritus from the surface of the granule using the medial edge setae. Dislodged particles are pushed posteriorly into the mouth by smaller mediolateral movements of the basipodites of the 1st maxillae. During this process the endopodites of the 2nd and 3rd maxillipeds manipulate the granule in such a way as to cause it to rotate such that its surface is brushed all over (Fig. 1 C). When thoroughly brushed, the granule is discarded and the process is repeated with a fresh granule.

3. Macrophagous Feeding. Soft material is held between the 3rd maxillipeds which press it against the inner mouthparts. The fingers of the 2nd maxillipeds work in alternation to push food backwards towards the mouth using the setae on the dactyl tip. The basipodites of the 1st maxillipeds and both pairs of maxillae are spread laterally allowing free access to the mouth. At the same time all three sets of appendages perform rapid mediolateral movements which cause the food to be abraded through the action of the setae on their medial edges. Periodically pieces of food are sliced off by the mandibles. During biting the inner mouthparts stop beating and the 1st maxillipeds and 2nd maxillae are spread laterally; the mandibles open and the 2nd maxillipeds push the food into the posterior buccal space. Posteriorly to the mandibles the food is grasped by the mandibular palps and

the labrum. Anteriorly the food is grasped by the basipodites of the 1st maxillae, by the dactyls of the 2nd maxillipeds and by the crista dentata of the 3rd maxillipeds. As the mandibles slice through the food, the 2nd and 3rd maxillipeds and the 1st maxillae pull it outwards. The severed piece is then pushed posteriorly into the mouth by the mandibular palps and the labrum.

D. Discussion

Pagurus rubricatus lives on gravelly sediments rich in skeletal material (Probert et al. 1979). Such a heterogeneous substratum offers a variety of food sources which this hermit crab is well adapted to exploit. Animal food is clearly the most energy rich of the various foods available and predation on small invertebrates if probably the most profitable mode of feeding in that it supplies the maximum gain for effort invested. While searching for prey however, *P. rubricatus* feeds on detritus obtained either directly from the sediment or by scrubbing gravel granules. In this way it further maximizes the return obtained, in terms of energy, for the effort expended in foraging.

With few exceptions hermit crabs have been found to be able to feed in a number of different ways and on diverse food sources (see Kunze and Anderson (1979) for a summary review). As in *P. rubricatus* this may be an adaptation to maximize the net rate of energy uptake by exploiting whatever food happens to be available as the hermit crab ranges over the substratum searching for its preferred food. It is likely that the success of hermit crabs as a group is related to their opportunistic feeding habits. Those species with a limited feeding repertoire are invariably those which do not encounter a wide spectrum of food types because of the specialized habitats they live in. Such species include *Paguritta harmsi* which lives in attached polychaete tubes (Schuhmacher 1977) or in pits in living coral colonies (Patton and Robertson 1980); *Discorsopagurus schmitti*, which lives in attached polychaete tubes (Caine 1980); *Calcinus verrilli* which lives in the attached shells of vermetid gastropods (Markham 1977) and *Isocheles wurdemanni* which lives in high wave energy environments (Caine 1978). All four species feed mainly by filtering particles from the water. Even these show some flexibility, however, since the last three mentioned also feed on detritus (Caine 1978; 1980; Markham 1977).

In detrivorous and macrophagous hermit crabs food is collected mainly by the pereiopods, especially the chelipeds, and sometimes by the 3rd maxillipeds. There is a great variety of form of the chelipeds in different species of hermit crabs and in some cases this has been related to feeding behaviour (e.g. Caine 1975). In *P. rubricatus* the minor chela with its expanded and flattened outer edge is adapted for digging shallow pits in the substratum while the concave ventral surface makes an efficient scoop for collecting sediment (Fig. 1). The strong major chela with its numerous rows of molariform teeth is well adapted for cracking molluscan shells open.

The 3rd maxillipeds also differ in structure from species to species,

mainly in the relative development of the crista dentata. This has been correlated with the degree of involvement of this structure in trituration of the food in different species; predominantly macrophagous or predatory forms having larger and more numerous teeth than do detrivorous or filter-feeding species (Caine 1975; Kunze and Anderson 1979). The other mouthparts are very similar in gross morphology in the different species of hermit crabs, however they differ markedly in both the type and density of setation.

The setation of the mouthparts of *P. rubricatus* is more complex than that described for any other hermit crab. This is not surprising considering the number of feeding techniques used by this species. The same set of appendages have to function in different ways depending on what type of food is being processed. For example the medial edge setae of the basipodites of the 1st maxillipeds form a screen separating the anterior and the mid-buccal spaces during detritus-feeding but function in abrading the food during macrophagous feeding and help in scouring detritus from gravel granules during 'gravel-scrubbing'. This multiplicity of functions is probably the reason for the fields of mixed setae found on many of the buccal appendages. The picture is further complicated by the fact that some of the mouthparts are used as cleaning organs and feeding and cleaning setae may occur in close proximity to each other, e.g. on the fingers of the 3rd maxillipeds (Fig. 7). Setal structure may, however, be correlated with function.

Setae which function in manipulating food, in gripping the food during cutting and in abrading soft material during macrophagous feeding are predominantly cuspidate, triserrate, triserrulate and plumodenticulate types. The cuspidate setae probably function like the prongs of a fork while the finely serrated setules of the other setal types prevent slippage when grasping the food and make efficient abrading structures. Setae whose function is to groom other appendages are mainly serrate types, the strong denticulations on these acting like the teeth of a comb. A variety of setae participate in forming screens. These are mainly setulated varieties. Screens function in retaining material in the buccal region by filling the gaps between appendages, and by forming the floor and walls of the various buccal spaces. Setal screens are also important in suspension-feeding (e.g. the screen formed by the setae of the endopodites of the 2nd and 3rd maxillipeds and associated structures) and in particle selection (e.g. the filter screen formed by the medial setae of the basipodites of the 1st maxillae). Finally, setal screens function in channelling the exhalant current, carrying rejected material away from the crab. Serrulate, serrate and plumodenticulate setae, particularly those forming a part of screens also have a self-cleaning function. Plumose setae extend surfaces and form gaskets while a number of setal types (serrate, serrulate, plumodenticulate) serve to lock appendages together. A few setae carry out specialized functions. These include the cuspidate grating setae of the basipodites of the 1st maxillae, the gravel-scrubbing simple setae of the basipodites of the 2nd maxillae and the 'plumose' cleaning setae of the inner face of the carpopodites of the 3rd maxillipeds (Fig. 7 B).

Kunze and Anderson (1979) have described the function of the mouth-

parts during feeding in *Clibanarius virescens* and in three other hermit crabs. This process was similar in all four species. In *C. virescens* as in *P. rubricatus* material collected by the chelae is brushed posteriorly by the dactyls of the endopodites of the 3rd maxillipeds; the 2nd maxillipeds then sweep this material off the 3rd maxillipeds and transfer it to the inner mouthparts. The function of the remaining mouthparts is different in the two species. In *C. virescens* the setae of the basipodites of the 1st maxillipeds rake off particles from the endopodites of the 2nd maxillipeds. The basipodites of the 1st maxillipeds are in turn raked by the endites of the 2nd maxillae. The 1st maxillae then transfer this material from the endites of the 2nd maxillae to the mouth. This is completely unlike *P. rubricatus* where the basipodites of the 1st maxillipeds form a screen separating the anterior from the mid-buccal space while the basipodites of the 1st maxillae form a filter grating in front of the mouth. The 2nd maxillae push particles through this grating or reject them depending on size. While several authors have implicated the maxillae as functioning in particle sorting (Roberts 1968; Greenwood 1972; Caine 1975; Kunze and Anderson 1979), the mechanism by which this is achieved has not been previously described. Given the great similarity in structure of the maxillae in different hermit crabs, it is likely that particle sorting in most species takes place in an analogous manner to that described here for *P. rubricatus*.

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