The Feeding Habits of the Galatheidea.

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With 7 Figures in the Text.

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INTRODUCTION.

ALTHOUGH the Galatheidea are conspicuous members of the Anomura and occur commonly both on the shore and in deeper water, no account has yet been given of the different methods of feeding which are found within the group.

While working at the Marine Biological Laboratory at Plymouth some time ago I became interested, as previous workers have been, in the curiously modified third maxillipeds of *Porcellana longicornis*, and decided to examine the mode of feeding in this and related forms.

My best thanks are due to Dr. E. J. Allen, F.R.S., of the Marine Biological Association, and to Professor J. H. Orton, of Liverpool University, for every help and encouragement, and also to Professor J. H. Ashworth, F.R.S., of Edinburgh University, for valuable criticism of the manuscript.

Previous Work.

Dalyell (1853) describes *Porcellana longicornis* as the "fanning or ventilating crab," and mentions the alternating see-sawing action of the third maxillipeds fringed with long hairs ; he associates the movements however with respiration. Gosse (1854) points out the use of the maxillipeds in feeding, comparing them with the legs of a barnacle. The account, though brief, is accurate. Zimmermann (1913) states that sweeping hairs are present on the terminal segments of the third maxillipeds in some of the Galatheidea. Potts (1915) compares the third maxillipeds of *P. longicornis* with those of Hapalocarcinus, which is said to feed in a similar way. He states that the stomach contains small unrecognisable fragments, a small proportion of planktonic organisms and occasionally pieces of algæ. Borradaile (1921) states that *P. longicornis* gathers suspended food by means of the long fringes on the third maxillipeds. He suggests that larger pieces may also be seized by the chelæ, but did not observe the process. Hunt (1925) classifies *P. longicornis* as a suspension feeder, and *Galathea nexa* as carnivorous. Orton (1927) observes that *P. longicornis* uses the third maxillipeds alternately, "like whips or lacrosse racquets," for catching suspended particles.

No account has, up to the present, been given of the feeding habits of any species of Galathea.

Bionomics.

The British Galatheidea occur both on the shore and in deeper water. *Galathea nexa*, *G. intermedia*, and *G. dispersa* occur only in deep water. *G. strigosa* can be found during very low tides in certain districts, but it is more commonly taken in deeper water. *G. squamifera* is widely distributed between tidemarks, usually below stones and in crevices.

Porcellana longicornis occurs in deep water in the Cellaria beds and in crevices of Lepralia, under stones and in the roots of Laminaria. It is also found commonly between tidemarks along with *P. platycheles*, which clings to the under surfaces of stones and hides in crevices in the rocks, relying on its protective coloration to escape detection. Zimmermann (1913) states that *P. longicornis* is found only in places scoured free from mud by the tide, while *P. platycheles* inhabits muddy areas. This is not universally the case ; in the Plymouth district, both at Rum Bay and on Looe Island, the two species may be found under the same stones, although in the crevices, where a thick deposit of mud accumulates, only *P. platycheles* is present.

A considerable difference exists in the degree of activity of the Galatheidæ and the Porcellanidæ. The Galatheas have retained greater freedom of movement, using their legs for leisurely progression and being also able to dart rapidly backwards through the water by means of violent flappings of their well-developed tails. The Porcellanas, on the other hand, have become more and more crab-like in appearance and adapted to a sedentary life in crevices and under stones. *P. longicornis* can still creep rapidly over the substratum and sometimes attempts to swim in a feeble manner by flapping its tail. *P. platycheles*, however, has become still more sedentary, scarcely moving, and relying on protective shape and coloration for safety.

Galathea dispersa has been chosen as a typical example of the Galatheidæ from which the other forms do not differ appreciably while *Porcellana longicornis* has been taken as typical of the Porcellanidæ.

STRUCTURE OF THE MOUTH-PARTS.

Galathea dispersa.

Third maxilliped.

The endopodite of the third maxilliped of *Galathea dispersa* is long and mobile (Fig. 1, a). The basal segment is not expanded to form a branchial plate and never fits tightly over the mouth ; it is, instead, long and narrow with a longitudinal crest on the dorsal side bearing a row of strong teeth. The second segment is also elongated and bears on its inner edge two rows of stout setæ. The third segment is short and broad, and carries a brush of setæ pointing dorsally and towards the middle line ; these form an ill-defined cleaning tuft which is used for freeing the antennæ and antennules from particles of dirt. The fourth segment also carries a number of serrated setæ pointing towards the middle line. The terminal segment is long in proportion to its breadth. On its distal end it bears a number of stout setæ, serrated along one edge with close-set teeth, admirably fitted for scraping small particles off the substratum. Covering these over so that they cannot be seen in a ventral view is a tuft of simple, curved setæ which follow the others in the food-collecting movements and sweep up all particles loosened by the serrated setæ. The segment is also provided on its median side with a short row of strong spines with blunt lateral projections.

In *Galathea squamifera* (Fig. 1, b) the arrangement is essentially the same, but the first segment is shorter and broader and the second, third, and fourth are fringed on their inner side with a row of long bipinnate hairs, foreshadowing the condition found in Porcellana. This intermediate condition of the maxillipeds is of considerable interest when it is realised that *G. squamifera* is intermediate in habit between *G. intermedia* and the Porcellanas, occurring with the latter below stones while *G. dispersa* lives openly on the sea floor.

Second maxilliped.

The second maxilliped is also elongated. The penultimate segment is provided with a median tuft of hairs, and the terminal segment is covered with long stout bristles, curved at the points, and provided with a double row of fine teeth.

a. b.

FIG. 1.—(*a*) Ventral view of the left third maxilliped of *Galathea dispersa* ×6.
(*b*) Ventral view of the left third maxilliped of *Galathea squamifera* ×6.

First maxilliped.

The first maxilliped is a thin plate imperfectly chitinised. The basal endite of the protopodite is thickened dorso-ventrally and provided with stout curved setæ directed dorsally into the mouth opening. The distal endite is flattened dorso-ventrally and provided with similar setæ, which, however, are directed at right angles to the others and overlap the mandibles.

Maxilla.

The maxilla is also plate-like and weakly chitinised. The two basal endites are provided with a row of stout setæ, curved dorsally towards the mouth, and are also fringed both dorsal and ventral to the seta-row with fine hairs. The two distal endites are similarly provided with hairs and setæ, but these are directed towards the middle line and cover over the mandibles.

Maxillule.

The small maxillule is weakly chitinised and the basal endite is provided with a fringe of close-set hairs covering over a row of curved setæ which are directed dorsally towards the mouth. The distal endite has similar hairs covering a row of short thick spines, which at the anterior angle give place to longer and slenderer setæ.

Mandible.

The mandible is strongly calcified and provided with a sharp incisor process separated from a smooth molar process by a deep groove. The

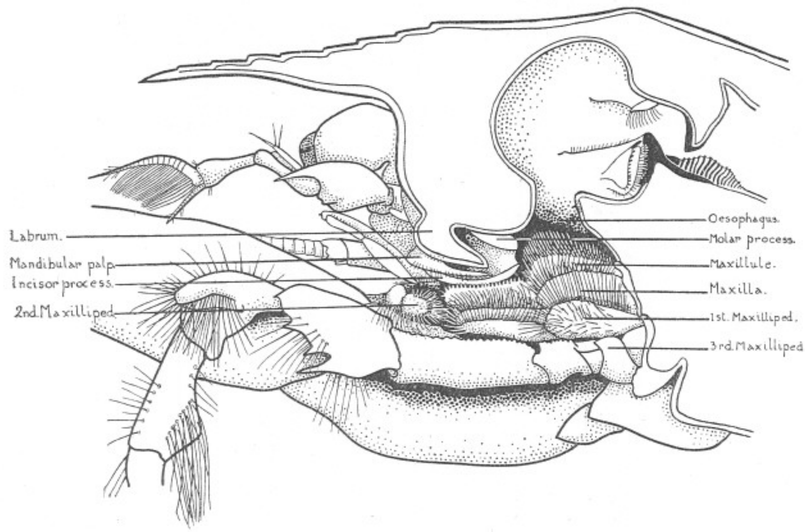

Fig. 2.—A median longitudinal section through *Galathea dispersa* to show the arrangement of the mouth-parts ×5.

palp is well developed and composed of three segments; the terminal segment is edged by a number of short spines.

In a median longitudinal section through the head (Fig. 2) the mouth is seen lying posterior to the mandibles. The labrum is median in position, and occupies, with the terminal segment of the mandibular palp, the groove between the incisor and molar processes. The mouth opening is bounded laterally by the dorsally-directed setose fringes of the proximal endites of the three pairs of inner mouth-parts, while the mandibles are covered over ventrally by the distal endites and their setæ, which are directed almost at right angles to those of the proximal endites.

Porcellana longicornis.

Third maxilliped.

The third maxilliped (Fig. 3) of Porcellana differs greatly from that of Galathea, and in certain respects approaches more nearly to the typical

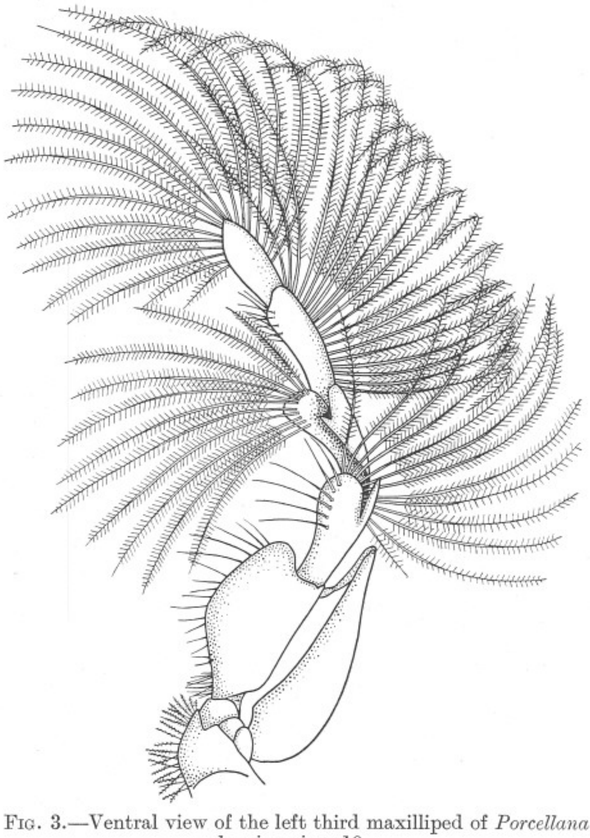

Fig. 3.—Ventral view of the left third maxilliped of *Porcellana longicornis* ×10.

Brachyuran type. The whole appendage is expanded laterally, but the three basal segments in particular have flattened expansions on their ventral surfaces. When the appendage is flexed between segments two and three, the distal part lies parallel and median to the basal part, and the fringing hairs of the last three segments, and in places the edges of the segments themselves, lie behind these lateral expansions so that when the two appendages are approximated in the middle line and pressed against the ventral surface, a serviceable opercular plate is formed. This plate plays no part in the feeding of the animal, as it does in Carcinus (Borradaile, 1922), but is formed as a protection to the mouth-parts at any sign of danger.

The first segment of the endopodite carries a few simple hairs. The second segment is fringed on its lateral margin by a number of very long pinnate setæ. The third segment bears a row of similar setæ on its median edge, while the fourth bears them on its lateral edge, and the fifth segment carries them on the median, terminal, and lateral margins. The result of this arrangement of setæ is that a spoon-shaped scoop is formed, extending over a relatively large area. The exopodite extends as far forward as the middle of the second segment.

Second maxilliped.

The second maxilliped is similar to that of Galathea, but the terminal tuft is longer and thicker and the setæ are pinnate, instead of being toothed.

First maxilliped.

The first maxilliped is less strongly chitinised than that of *Galathea dispersa*. The basal endite of the protopodite is fringed with long, weak setæ, curved dorsally towards the mouth and overlapped ventrally by a row of fine hairs. The distal endite is covered with fine setæ which are directed towards the mid-ventral line. The endopodite is composed of two segments ; the more distal is bare, but the other is fringed with delicate setæ.

Maxilla.

The maxilla is also weakly chitinised. The proximal endite bears a number of stout setæ curved towards the mouth and covered over ventrally with long hairs pointing in the same direction. Each of the three distal endites is fringed with a brush of soft hairs.

Maxillule.

The proximal endite of the maxillule bears a dense fringe of fine setæ which are curved towards the dorsal surface and point into the mouth. These are covered ventrally by a row of hairs. The distal endite is fringed with shorter and stouter setæ directed towards the middle line.

Mandible.

The mandible does not differ except in size and the arrangement of the teeth of the incisor process from that of *Galathea dispersa.*

FEEDING HABITS.

Galathea dispersa.

The food taken by the Galatheidæ is of two sorts; large pieces of animal and vegetable material, or organic debris and micro-organisms from the deposits of the sea bottom.

An examination of the stomach contents of members of the Galatheidæ shows that the deposit-feeding method is the more usual. The species examined were *G. squamifera*, *G. strigosa*, *G. dispersa*, and *Munida rondeletii.* Always the bulk of the stomach contents was found to consist of unidentifiable detritus, fine sand, small pieces of red and green algæ, a few diatoms and unicellular algæ, parts of small crustacea, eggs, and small gastropods. In addition pieces of muscle and larger pieces of algæ were found in small quantities, showing that the animals had also been feeding on larger material. *G. dispersa* can be taken as a typical example.

Deposit feeding.

When Galathea is feeding on finely divided material the third maxillipeds are used for collecting food, and act as brooms which sweep over the substratum, into grooves and hollows, over the animal's own legs or those of its companions, and collect the diatoms, small animals, algæ, and detritus which may be there. The maxillipeds are extremely mobile at all joints, and capable of being extended both anteriorly and laterally for a considerable distance. When in use for collecting material lying on the substratum in front of the animal, they are stretched out to their fullest extent, and their tips are then pressed against the substratum, often so tightly that the terminal setæ are bent almost at right angles to the segment, as they are drawn back towards the mouth (Fig. 4). The maxillipeds are most frequently used together, but they can also work alternately. If only a small quantity of material has been collected it is lifted from the substratum in the terminal tufts of the appendages and brushed out by the second maxillipeds. If a large amount of material has been gathered, it is lifted between the terminal segments of the third maxillipeds. The substratum below the ventral surface of the animal can also be swept by the maxillipeds, which are bent then ventrally from the base and posteriorly from the second joint of the endopodite so that the opposite side of the setal tuft is used to sweep over the substratum in an anterior direction.

When the brushing movement of each maxilliped is completed, it is folded upon itself so that the third segment of the endopodite is at right angles to the other parts of the limb, and the terminal segments are lying in a plane parallel to the basal segments, but nearer to the midventral line. In this position it is easier for the relatively short second maxillipeds to reach all the setæ.

The second maxillipeds always work alternately. The terminal segments of their endopodites are stretched anteriorly, and their terminal

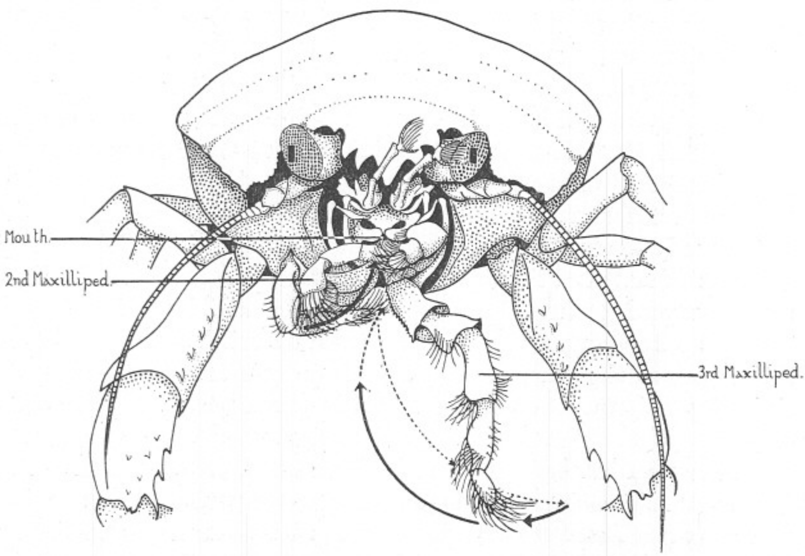

Fig. 4.—An anterior view of *Galathea dispersa* in the act of feeding on finely divided material. The left third maxilliped is fully extended and is collecting particles off the substratum; the right is flexed and the bristle bundles are about to be cleaned out by the second maxilliped. The left second maxilliped has completed the cleaning movement and is carrying the food between the inner mouth-parts to the mouth, ×4. The continuous arrows show the path of the second maxillipeds and of the third when on the substratum; the dotted arrows show the path of the latter through the water.

setæ inserted into the tufts on the third maxillipeds. They are then drawn back towards the mouth and their tips twisted ventral to, and between, their own bases where they are combed out by the inner mouth-parts (Fig. 4). Some kind of sorting mechanism is formed by these appendages, so that suitable particles are allowed to pass to the mouth while unsuitable material is thrust into the outgoing respiratory current made by the flagella of the exopodites of the two pairs of maxillipeds. Since the inner mouth-parts all lie on top of each other, and are partially obscured by the maxillipeds, it is not possible to observe the process of sorting.

Feeding on large pieces of food.

The power to detect food at a distance is not well shown in Galathea, under aquarium conditions at any rate, for pieces of fish or mussel which are out of reach of the chelæ are disregarded. When, however, food is presented to a Galathea at close range, several methods may be employed to convey it to the mouth. If the piece is large it may be seized in one chela while small pieces are pulled off by the other and passed to the maxillipeds. If the piece is small it may be passed direct to the maxillipeds, one or both of which may receive it. If very small it may be brushed out from between the pincers by the terminal brush of one maxilliped and passed direct to the mouth. If larger it may be grasped by the cleaning tufts of both the third maxillipeds and passed on to the second maxillipeds. Usually the cleaning tufts of the third maxillipeds retain a loose hold of the food, while the terminal segments are folded towards each other in the middle line and form a floor to the feeding chamber, ready to exert pressure on the food when required. The second maxillipeds do not pass the food further towards the mouth, but rotate it until a ragged corner is presented to the mandibles. The second maxillipeds take up a position with the terminal bristle bundles inserted into the food, so that they can push it away from the mouth and thus work in opposition to the third maxillipeds which press it closer to the mandibles.

When the piece has been arranged by the second maxillipeds the mandibles prepare for action. The incisor processes separate, the palps and labrum are raised, and the food is pushed in between the mandibles by the pressure of the third maxillipeds. The mandibles then close and the palps and labrum are slightly lowered. The action of the incisor processes is not usually so much a tearing action, as described for other forms, as an actual cutting movement, which takes place in three phases; the edges close on the food; pressure is exerted (shown by a pause); the mandibles overlap suddenly as they cut through. If the food is tough it may be pulled away by the second maxillipeds while the mandibles grip it, so that tearing does take place under certain circumstances. The subsequent events depend on the nature of the food. Soft material like the body of the polychæte Pomatoceros is bitten through several times without any tearing action, the whole piece being pushed further in between each bite and rapidly swallowed. Tougher material like the anterior end of the worm, which contains an internal supporting structure, is treated differently. Between each bite, which is assisted by the tearing action of the second maxillipeds, the palps and labrum descend, pushing the material up into the œsophagus and cleaning out the groove behind the cutting edge of the mandible. The piece is presented again to the mandibles, either in the same position as before or after rearrangement. When the operculum of the worm is presented to the mandibles it is rotated many times and attempted from many angles before it can be cut through by the mandibles, although it is finally divided into four or five pieces and swallowed.

The inner mouth-parts appear to assist in retaining the food in position in front of the mandibles, but make no obvious or well-defined movements.

Porcellana longicornis.

The Porcellanidæ have abandoned the deposit feeding habits of the Galatheidæ, and also to a great extent the method of feeding on large particles, although the mandibles show no corresponding weakening of structure. Only once was a *Porcellana longicornis* observed to pass an object of any size to the mouth-parts. A small mollusc became attached to a chela and was removed by the third maxillipeds, presented to the inner mouth-parts and rejected at once in the respiratory current. Whether this was an act of feeding or merely a cleaning reaction is not certain, but appears more likely to have been the latter. On the other hand, Dalyell reports that Porcellana occasionally eats mussel in captivity, and Potts found relatively large pieces of algæ in the stomach. This observation was not confirmed either on material from deep water at Plymouth or from shore specimens from the Firth of Forth. In both cases Hunt's statement that the food of these animals consists of detritus and micro-organisms, closely comparable to that of filter-feeding ciliary feeders, was confirmed. No difference was found between the food or the method of obtaining it in *P. longicornis* and *P. platycheles*, so that the former, which is more easy to observe, has been taken as the type.

The Feeding Mechanism.

The respiratory current plays an important part in the feeding of *P. longicornis*. In contrast to Galathea where the flagella of the exopodites of both sides beat at the same time, in Porcellana they function alternately, so that water is drawn across the front of the carapace and can easily be tested by the antennules. Up to the present it has not been found possible to determine the nature of the stimulus which starts the feeding movements. The animals rarely fed in the morning unless after several days' starvation, but in the afternoon the addition of fine plankton or ground-up algæ to the water was often sufficient to start the process. This curious observation is substantiated by Dalyell's statement that the " ventilating movements " were always more active in the afternoon.

The direction of the respiratory current is shown in Figure 5, when the flagella of the right side alone are beating. As the abdomen of the crab is

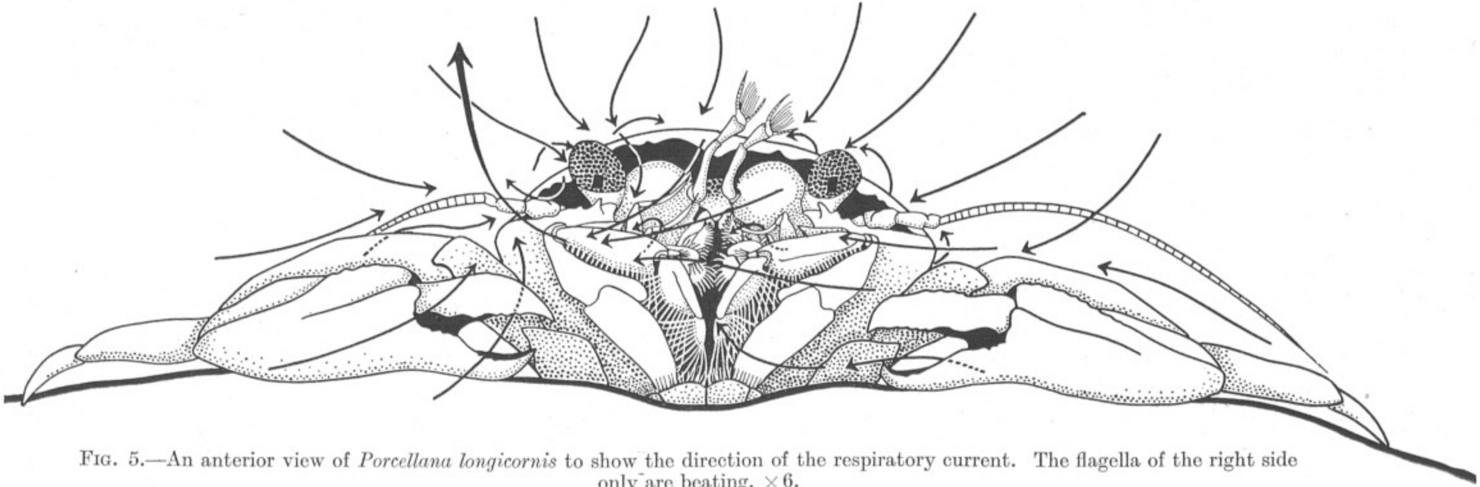

FIG. 5.—An anterior view of *Porcellana longicornis* to show the direction of the respiratory current. The flagella of the right side only are beating, ×6.

held pressed against the substratum no water is drawn over the ventral surface, but a strong current passes anteriorly over the dorsal surface. Water from the animal's left passes behind the chela of that side under the eye and antennules and across the maxillipeds, where it is joined by the water bailed out of the left branchial chamber by the action of the scaphognathite. Water from the anterior direction and from the dorsal surface of the animal on that side passes under the antennules, which are turned towards the left and flick and jerk continually. Water from the right side passes round the antennule and eye as on the other side, but before it reaches the flagella it is turned aside in an antero-lateral direction by the stream of water leaving the right flagella and derived partly from the left side of the body and partly from the right branchial cavity. Water from

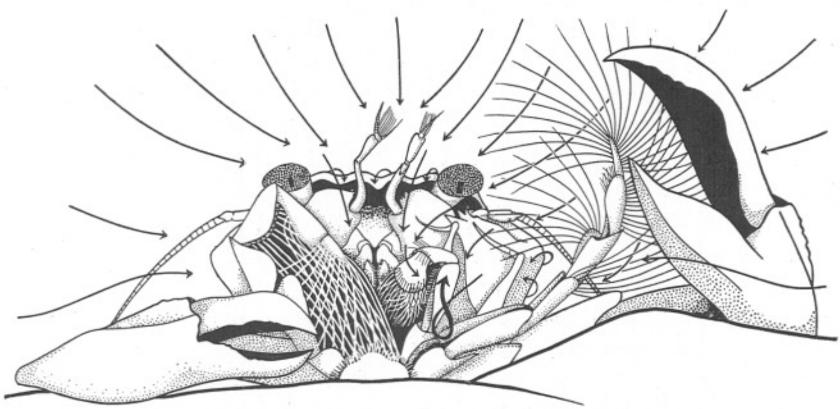

FIG. 6.—An anterior view of *Porcellana longicornis* while feeding, to show the direction of the water currents drawing food in suspension towards the animal, rapidly on the left side, more slowly on its right where the maxilliped is flexed, ×5.

the left branchial cavity joins the main stream of water from that side. Water passing forward over the dorsal surface travels in an anterior direction to the edge of the carapace, where it passes round the eyes and antennæ to join the main streams from the sides.

After a longer or shorter period the flagella of the other side begin to beat spasmodically, and after a few seconds a complete reversal of the current takes place, the left flagella alone beating.

By this means the water round the animal is kept in constant motion, particles in suspension are drawn into contact with the antennules, and the animal is made aware of the presence of suitable food in the neighbourhood.

As soon, however, as feeding commences the beating of the flagella ceases altogether, and another water current, formed by the movements of the third maxillipeds, is set up (Fig. 6). When a feeding animal is looked at from in front, particles in suspension in the water can be seen moving towards the mouth symmetrically from all directions except from below. Water is also drawn anteriorly over the dorsal surface, and the whole mass is turned away from the mouth in an antero-lateral direction. The current is not of equal intensity on both sides of the body at the same time, owing to the alternate movements of the maxillipeds. The flexing of the maxilliped of one side causes the traction to cease, although the momentum of the water mass continues the movement while the maxilliped is unfolding again, but at a slower rate.

The capture of food is brought about entirely by the movements of the third maxillipeds. Their bases are attached on either side of the middle line and are free to move laterally through about 60° and dorso-ventrally through about 30°. When feeding commences the maxillipeds are lowered to their greatest extent (Fig. 7, a) and are then swung laterally to the limits of their movement without being unbent. When, however, they reach that point the terminal joints are unflexed, and the setæ edging them spread into position (Fig. 7, b). These hairs appear to be under muscular control. This can best be seen in a Porcellana when, with one maxilliped half-unbent, the feeding act has been suspended by some movement which disturbs the crab. When the limb is flexed the hairs on any segment lie parallel and close together, but when it is extended the hairs diverge to form an extensive net. Under the circumstances a gap is often apparent in the row of hairs when those towards the distal end have taken up their spread position, while those towards the proximal end are still parallel. Often it is possible to see one or more hairs leave the parallel series and move across the gap into position beside the others. As the feeding recommences the rest of the hairs spread out also. When the maxilliped is fully extended the hairs stand out for a considerable distance, so that a large spoon-shaped net is produced whose walls are formed by the hairs and their lateral branches. This net projects a considerable distance beyond the front of the carapace and covers a large area. As the maxilliped is flexed the basal segments move towards the middle line through an angle of about 30°. As the hairs come together a considerable volume of water passes between them and many of the particles in suspension are filtered out. The maxillipeds usually move alternately, one being fully flexed while the other is fully extended, but often over long periods of time only one will work, the other remaining in the flexed position.

The movements of the second maxillipeds are closely correlated with those of the third. As soon as one of these appendages is flexed then the basal segment of the second maxilliped on that side is moved through a small angle away from the middle line, and the distal segments are rotated anteriorly and laterally so that the terminal brush of setæ can be inserted into the bases of the series of hairs on the third maxilliped

(Fig. 7, c). The distal segments are then rotated back again into a position with the tips tucked under and into the mouth, while the third maxilliped is turned laterally and again unflexed so that the whole length of the hairs

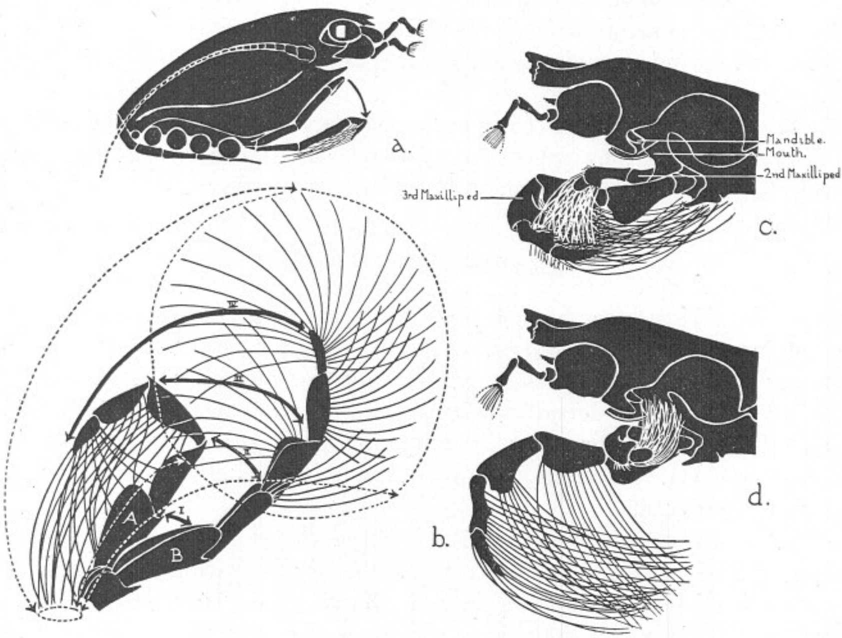

FIG. 7.—(*a*) A lateral view of *Porcellana longicornis* to show the lowering of the third maxillipeds at the commencement of feeding, ×4.

(*b*) A ventral view of a third maxilliped in two positions, A when flexed at the beginning and end of each feeding movement, B when fully extended. The continuous arrows indicate the paths taken by the segments of the appendage as it alternates between positions A and B. The movements indicated by arrows I and II are completed simultaneously and are then followed by III and IV in quick succession, when the limb is being unflexed. When the limb is being flexed the movements follow each other evenly in the reverse sequence. The dotted arrows indicate the movements of the hairs of the filter-net, ×7.

(*c*) A median section through *P. longicornis* to show the relative positions of the second and third maxillipeds at the end of each feeding movement. The third maxilliped is fully flexed and the second fully extended, the hairs on the two interlocking, ×6.

(*d*) A median section through *P. longicornis* to show the relative positions of the maxillipeds at the end of the combing movement of the second maxilliped. The third maxilliped is spreading out again and the second is fully flexed presenting the food collected from the hairs of the third maxilliped to the inner appendages and the mouth, ×6.

on it is drawn through the terminal brush of the second maxilliped (Fig. 7, d). If a great many particles have been caught one brushing may not be enough, and the regular cycle of movements is interrupted while the hairs are combed out several times in succession. The second maxilliped is then tucked in between the inner mouth-parts and withdrawn at the same time as its neighbour from the other side approaches. The result is that each maxilliped is combed out by the other one as well as by the inner mouth-parts. That this is of considerable importance in feeding is shown by the fact that when one casting net only is being used both the second maxillipeds are working and the food is pushed from one to the other.

The exact function of the inner mouth-parts is again obscured by the maxillipeds, but they appear to select and sort the food as in Galathea, rejected material being shaken off and carried away in the respiratory stream.

CLEANING MOVEMENTS.

In the Galatheidea the fifth pair of legs are closely concerned with the cleaning of the carapace both inside and outside. Although reduced in many ways they are specially adapted for this purpose by their length, being able to reach dorsally as far as the eyes and ventrally as far as the maxillipeds, by their great mobility and by the presence of a small grasping chela. In addition a tuft of sickle hairs is present as described by Zimmermann.

In the Galatheidæ the fifth leg is often thrust inside the branchial cavity and under the posterior margin of the carapace to remove small particles which have lodged there. The appendage is then stretched forward on the ventral surface to the third maxillipeds, whose terminal tufts sweep it clean. It is also used for cleaning the ventral surface of the telson, the dorsal surface of the carapace, and the posterior appendages. The anterior appendages are cleaned on the ventral surface by the terminal brush of the maxillipeds which stretch far out in order to reach them, on the dorsal surface by the fifth leg. The antennules are cleaned by being bent sharply down and pulled several times through the cleaning tufts of the third maxillipeds. These are brought together parallel to each other in the middle line with the last three segments bent downwards, and the setæ of the cleaning tufts locked together round the antennule. They are then moved away from the ventral surface, while the antennule passes back into position. The antennæ are cleaned in a similar manner, but all the hairs of the third maxillipeds take part, the antenna being drawn along the length of the appendages. After each cleaning movement is completed the third maxillipeds are carefully brushed out by the second maxillipeds and any small food particles are sorted out and swallowed, the rest being rejected.

In the Porcellanidæ the cleaning process is in essentials the same as in the Galatheidæ, except that the fifth legs are used for cleaning both the dorsal and the ventral surface of the appendages and then presented direct to the second maxillipeds for cleaning, since the setæ of the third maxillipeds are unsuited for this purpose.

Although the bulk of the material collected from the surface of the animal is unsuitable for food, and is at once rejected, a certain amount of edible material is swallowed, so that the cleaning movements serve the double purpose of removing dirt from the carapace and supplying the animal with food.

DISCUSSION.

Little is known about the feeding habits of other members of the Galatheidea, and since the structure of the third maxillipeds is not of importance in classification, few drawings sufficiently detailed to deduce from them the method of feeding can be found in the literature on Crustacea. Laurie (1926), however, gives a drawing of the maxilliped of *Pterolythes alobatus*, which is almost identical with that of *Porcellana platycheles*, and leaves no doubt that the method of capturing food is the same.

In other groups of the Anomura almost as little is known of the feeding habits.

In *Eupagurus bernhardus* the third maxillipeds are used in a similar way to those of Galathea (Orton, 1927). They are long and do not form an opercular plate, but sweep up particles from the bottom by means of a terminal brush of setæ. In addition the small chela is used to scrape up deposited material and pass it to the maxillipeds. Large pieces of food are also passed to the maxillipeds by the chela. The mouth-parts are poorly adapted for dividing large masses of food and small pieces are cut off with difficulty so that the bulk disappears very slowly.

Uca leptodactyla feeds upon minute organisms and organic debris which it scrapes off the sand particles in front of its burrow when the tide goes out (Matthews, 1930). The sand grains are picked up one at a time by the small chela and presented to the mouth-parts. The first and second maxillipeds are provided on their median edges with long bristles, many with spatulate ends, and it is by means of these that the sand grains are scoured.

Birgus latro has become adapted to living on land and feeds on coconuts (Darwin, 1860). The husk is peeled away and one of the eye-holes battered in with the large claw. The last pair of walking legs are provided with small narrow pincers, and these are then used to extract the food.

Upogebia pugettensis feeds entirely on suspended matter owing to its specialised habitat (MacGinitie, 1930). The animals live in burrows with constricted openings through which they cannot pass and subsist entirely on plankton, large masses of food being rejected. The water current containing the suspended matter is drawn in by the action of the swimmerets and filtered on the hairs edging the first trunk limbs. The third maxillipeds are here modified as combs to clean the filtering hairs. They work alternately and are in turn cleaned out by the second maxillipeds.

Although a more detailed comparison cannot be carried out at present, it has been shown that in members of three out of the four subdivisions of the Anomura the typical carnivorous habit of the Decapoda has been given up or reduced in importance, and secondary methods of feeding adopted, first on bottom deposits and by still greater modification on plankton, and it is probable that there is a general tendency throughout the group to feed on fine particles of food.

In the majority of the Brachyura the third maxillipeds have lost their length and mobility, and form the relatively rigid opercular plate, but an examination of the gut contents of slow-moving crabs such as Macropodia, Inachus, and Hyas, shows that in some deposit-feeding plays a considerable part. In order to check the results obtained from examining the gut contents, several specimens of Inachus, Macropodia, *Galathea squamifera*, and *G. dispersa* were placed together in a dish containing sand, detritus, diatoms, and general vegetable matter from the sides of an aquarium tank. At the end of three hours the gut contents were examined. Inachus and both species of Galathea showed similar gut contents, very fine sand, short lengths of red and green algæ, detritus, diatoms, and unicellular plants, resembling closely the stomach contents found under natural conditions. When observed alive, Inachus was seen to pick up minute particles in the chelæ and hold them in front of the mouth where the maxillipeds brushed them from between the pincers and were in turn brushed out by the second maxillipeds which fold below the mandibles into the mouth. Macropodia had eaten nothing. This agreed with the observations on the natural food of the animal. The stomach contents show that it is a carnivorous selector, feeding almost exclusively on small crustacea, the stomachs of many examined being filled with the remains of copepods and ostracods. This type of food was not supplied to the animals under observation, so that they did not feed.

Hyas in captivity will eat mussel readily, and can be seen picking up small pieces of food with the chelæ. An examination of the gut contents suggests that the animal is only to a small extent a deposit-feeder, eating small Polychætes, pieces of Ophiuroids, and algæ mixed with a certain small amount of sand and organic debris.

One member of the Brachyura is of particular interest, Hapalocarcinus, the gall-forming crab, which spends its life shut up in a chamber in the coral into which only matter suspended in the water can enter. The mouth-parts and probable method of feeding have been described by Potts (1915) from preserved material. The third maxillipeds are closely fringed with hairs and serve to strain plankton from the water entering the gall. Hapalocarcinus differs however from Porcellana in the great reduction of the inner mouth-parts.

The well-developed mouth-parts of the majority of the Decapoda show that they were originally carnivorous, feeding on large food masses. Departures from the normal methods of obtaining food are entirely secondary, and have been developed independently in various groups, often in connection with peculiar habitats.

SUMMARY.

The Galatheidea are divided into two families, the Galatheidæ and the Porcellanidæ, which differ from each other in their feeding habits as well as their structure.

Galathea dispersa has been taken as typical of the Galatheidæ. An examination of the gut contents shows that the food in the stomach consists of finely divided particles mixed with sand and detritus. In addition larger pieces of animal and vegetable matter are occasionally found. Observations of the animals in captivity show that they feed by two methods ; either large pieces of food are seized by the chelæ and maxillipeds and passed to the mandibles or, as is more usual, the third maxillipeds are used to collect finely divided material from the substratum. The setæ on the terminal segments of the maxillipeds form a dense tuft which sweeps over the substratum, loosening and collecting small particles. The terminal tufts are cleaned out by the setæ of the second maxillipeds, and the food passed to the mouth.

Porcellana longicornis has been taken as typical of the Porcellanidæ. The stomach contents are much more finely divided than those of Galathea, and are closely comparable to those of the filter-feeding polychætes and molluscs. The third maxillipeds are fringed with long bipinnate hairs which stand out to form a large spoon-shaped scoop. The appendages are swung sideways alternately, unfolding and spreading the setæ. They are then flexed again as they move back towards the middle line, entangling particles in suspension in the water in the setæ which are in turn brushed out by the second maxillipeds and the food passed to the mouth.

It is evident that the Galatheidea have largely abandoned the predatory habits of the rest of the Decapoda, a change which has also occurred in members of other groups of the Anomura such as the Hermit Crabs and the Mud-shrimp, Upogebia.

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