NOTES ON CERTAIN ASPECTS OF THE BIOLOGY OF *CUMOPSIS GOODSIRI* (VAN BENEDEN) AND SOME OTHER CUMACEANS IN RELATION TO THEIR ENVIRONMENT

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(Text-figs. 1-7)

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INTRODUCTION

The results of observations on limb movements concerned with feeding, breathing, swimming, burrowing and cleaning are recorded. From the study of the habits and functional morphology of certain Cumacea, particularly *Cumopsis goodsiri* (van Beneden), the importance of some ecological factors is deduced, and the extent to which they may control the intertidal zonation of these forms is discussed.

Recent literature dealing with the habits and habitats of the Cumacea includes Dennell's (1934) account of the feeding mechanism in *Diastylis* bradyi Norman, Zimmer (1932) on the habits of *Diastylis rathkei* (Kröyer), *Iphinöe trispinosa* (Goodsir), *Lamprops fasciata* Sars, and *Pseudocuma* sp. Foxon (1936) has also described observations made on the last three forms mentioned.

I should like to thank Dr E. E. Watkin, D.Sc., for helpful criticism during the course of the work.

DISTRIBUTION AND METHOD OF COLLECTION

Within recent years several investigations have been made on the distribution of sand fauna in Great Britain, and these include a few references to *Cumopsis*. This sand-dwelling genus is, however, probably one of the most common

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Cumacean forms occurring on our shores, and the scarcity of records concerning it may be due to the difficulty experienced in its collection, as the small size of the animal enables it to pass through the mesh of the standard sieves used in these researches. The specimens used in the present work were collected from the sandy beaches of Kames Bay, Millport, Buteshire; Oxwich Bay, Gower, Glamorgan; and Aberystwyth, Cardiganshire.

Sars (1879) describes *C. goodsiri* as a marked littoral form, but the collection of this species at Kames Bay, Oxwich Bay and Tenby, Pembrokeshire, showed its distribution to be confined within the neap-tide range. At Oxwich Bay and Tenby the zonation ranged from a little above M.S.L. to L.W.M.O.N.T., disappearing altogether as spring-tide levels were reached. The term 'littoral' is better applied to *Bodotria scorpioides* (Montagu), as it occurs in Aberystwyth. Here the shore is typically rocky and the intertidal zone is made up of shingle. This shingle becomes gradually finer as the L.W.M.S.T. level is approached and at this point there is a narrow strip of sand, partly exposed at L.S.T., but nearly always covered by shallow water.

The animals may either be collected from the water during swarming periods, or from the sand normally. In this investigation they were collected from the soil, and the method already described by Foxon (1936) was used. The surface inch of sand was placed in a bucket and covered with sea water. A gentle stirring of the sand disturbed the animals, and caused them to swim in the surface water, which was quickly filtered through a muslin net. At Aberystwyth *B. scorpioides* had to be collected from shallow water, where the sand was covered with a thin layer of shingle and contained a high percentage of detritus, which made the use of a muslin net impracticable. Instead the substratum was stirred, and the resulting cloudy water sieved. Only large specimens were caught in this way.

RESPIRATION

Cumopsis goodsiri has well-developed gill chambers on either side of the thorax. Zimmer (1932) has described these chambers in *Diastylis rathkei*, and in principle his description holds for all Cumacea. Each chamber is oval in shape, with its roof, outer lateral walls, and floor formed by the branchiostegite (Fig. 1). The respiratory apparatus lying within is divided into two regions, the anterior siphonal, and the posterior gill regions. The exopodite of the first maxillipede forms the siphonal region. It is composed of a broad chitinous band whose edges curl together to form a narrow expiratory siphon, which is slightly tumose at the distal end. The latter part appears periodically outside the pseudorostral chamber. The gill region lies posteriorly, and within it are 12–15 delicate, foliaceous gills which arise from a median longitudinal hollow, on the boat-like epipodite of the first maxillipede. They graduate from large anterior to small posterior gills. In situ the floor of the epipodite lies ventrally and the gills are inclined dorsally. A thin chitinous fold arises from the floor of the epipodite in the median line and curves over laterally until

its edges come in contact with the incurving ventral portion of the branchiostegite (Fig. 1, i, mf). Together the fold of the epipodite and the incurving portion of the branchiostegite form the floor of the gill chamber. There are two openings into the latter. The anterior opening is guarded by the expiratory siphon and the posterior one by the basis of the third maxillipede. It is

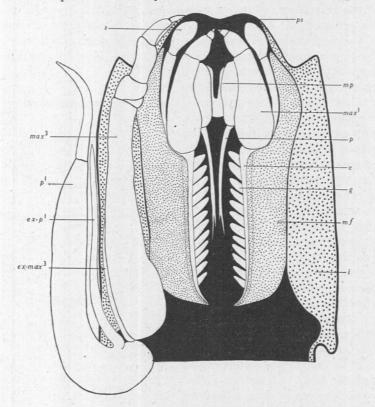


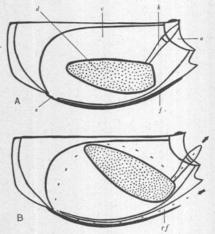
Fig. I. A diagram of the ventral view of the thorax of *C. goodsiri* (van Beneden), showing the position of the respiratory organs. *e*, epipodite; *ex-max*³, exopodite of the 3rd maxillipede; *ex-p*¹, exopodite of the 1st peraeopod; *g*, gills; *i*, incurving part of the branchiostegite; *max*¹ and *max*³, 1st and 3rd maxillipedes; *mf*, membraneous fold of the epipodite of the 1st maxillipede; *mp*, mouth parts; *p*, maxillulary palp; *p*¹, 1st peraeopod; *ps*, pseudorostral chamber; *s*, expiratory siphon.

possible to observe the breathing mechanism by using a dilute suspension of carmine in sea water. The water enters the gill chamber posteriorly at the base of the third maxillipede, and leaves anteriorly through the expiratory siphon (Fig. 2 A, B). During respiration the third maxillipede is depressed away from the body to form a funnel through which the inspiratory current flows (Fig. 2 B) directed by the rhythmic movements of the exopodite of the third maxillipede (Fig. 1). There are two aspects of inspiration. At times the third maxillipede is depressed only slightly away from the body, so that the funnel

opening is small and the ingoing current passes slowly into the gill chamber. The only activity within the chamber is the constant movement of the maxillulary palp, which lies towards the inside of the gills (Fig. 1). This keeps up a circulation of water over the gills, and thus prevents the water inside the gill chamber from becoming stagnant. During this time no water is seen to leave through the expiratory siphon. But spasmodically inspiration becomes rapid and very pronounced. The third maxillipede is considerably depressed and there is a violent inrush of water into the gill chamber, which tilts the gill apparatus into a more vertical position (Fig. 2B). This initiates a series of

movements of the gill apparatus. As fresh water enters ventrally some of the water already in the chamber is forced out by the gill apparatus dorsally through the expiratory siphon and in this way the gill chamber is flushed at intervals.

These animals live in a habitat which has a very high detritus content, and the inspiratory stream as a result carries a quantity of fine material in suspension. The latter is prevented from entering the gill chamber and causing asphyxiation by the long feathered bristles on the basis of the third maxillipede (Fig. 5A), which form a sieve over the funnel opening to filter the particles from the inspiratory current. These bristles lie normally curled inwards between the body wall and the inside of the basis, tory activity. *a*, pseudorostral chamber; *b*, expiratory siphon; *c*, gill chamber; *d*, it expiratory into the gill but, when the maxillipede is depressed away from the body, they uncurl so that their setules overlap to form a network



gill apparatus; *e*, opening into the gill chamber at the base of the 3rd maxillipede; f, 3rd maxillipede; rf, respiratory funnel.

over the funnel opening. This filtering process is probably important from the ecological standpoint, as the size of the particle that can be effectively filtered will depend upon the size of the holes in the mesh of the sieve. The quality of the feathering of these bristles differs in the respective species of the Cumacea. Thus Cumopsis goodsiri has a coarse sieve, whilst the sieves of Bodotria scorpioides and Iphinöe trispinosa are comparatively fine. The Diastylidae have very finely feathered bristles and therefore possess fine sieves. To a certain extent it is known that the species mentioned live in specific soil grades. Cumopsis goodsiri occurred at Oxwich Bay in greatest abundance around M.S.L. and gradually thinned out as L.W.M. and a finer soil grade were reached. At Aberystwyth Bodotria scorpioides inhabited fine grade sand containing abundant detritus. Watkin (1942), in a survey made at Kames Bay, found the Cumopsis goodsiri zone to range from M.S.L.O.N.T. to L.W.M.O.N.T.

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and Iphinöe trispinosa from L.W.M.O.N.T. to shallow water. From an analysis of soil grade in this case it was found that Cumopsis goodsiri inhabited a coarser soil than Iphinöe trispinosa. The Diastylidae generally favour muddy soils and therefore need fine sieves. Thus, from the facts available so far along these lines, it seems that soil grade in connexion with the respiratory activities is a factor which helps to confine these species to certain zones within the intertidal area.

FEEDING

The Cumacea feed on micro-organisms which occur in the soil detritus, and the manner of food collection depends upon the nature of the substratum. Mud-dwelling species filter small particles in suspension, and sand dwellers clean their food off sand grains and other small objects. Cumopsis goodsiri belongs to the last category.

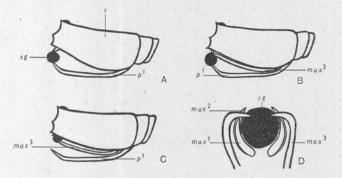


Fig. 3. Diagrammatic illustrations of some of the feeding movements of *C. goodsiri.* c, cephalothorax; max^1 to max^3 , 1st, 2nd and 3rd maxillipedes; p^1 , 1st peraeopod; sg, sand grain.

The feeding mechanism is best observed when the animals are placed in a watch glass containing sea water, a few scattered sand grains, and bits of decaying plant matter. The objects which carry the food are picked up by the first peraeopods and passed on to the third maxillipedes. The food is then cleaned off by the first and second pairs of maxillipedes, and conveyed to the mouth by the true mouth parts, maxillae, maxillules and mandibles. The mouth with the mandibles on either side lies at the bottom of a slight depression, and all the other appendages mentioned lie one on top of the other terminating with the first peraeopods. Cumopsis is a selective feeder and carefully searches the substratum for food with its first peraeopods. These then pick up the grain bearing the food (Fig. 3A) and pass it to the third maxillipedes, whose endopodites flick backwards to receive it (Fig. 3 B, C). If it happens to be very heavy the first peraeopods will retain their hold as well and in this way objects almost as big as the cephalothorax are handled. The first and second maxillipedes prepare to clean the grain by arranging their endopodites into a cup-shaped hollow, into which the third maxillipedes fix the grain (Fig. 3D), and in so doing bring it in contact with the armature on the 5

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walls of the hollow (Fig. 4). Then the first and second maxillipedes begin a saw-like movement which serves to scrape off any material clinging on to the surface of the grain. The third maxillipedes occasionally rotate the grain in the hollow to expose all its surfaces, and when it has been well cleaned it is discarded. Methods of grain disposal in other Cumacean species have been described by Zimmer (1932) and Foxon (1936). In *Pseudocuma* the grains are shot backwards over the dorsal surface of the body, in such a way that in time the grain cleaning leads to the formation of a hollow in the soil in front of the animal.

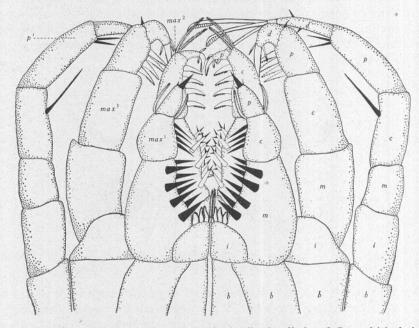


Fig. 4. Armature on the distal parts of the food-collecting limbs of C. goodsiri. b, basis; c, carpus; d, dactylus; i, ischium; m, merus; max¹ to max³, maxillipedes; p, propodus; p¹, 1st peraeopod.

In *Cumopsis* the third maxillipedes merely relaxed their hold on the grain, and it dropped in front of the animal. Sometimes it was shot backwards over the dorsal surface of the carapace as described above for *Pseudocuma*, but this movement was not normal and coincided with the respiratory activities. Thus often the third maxillipedes retain their hold on the grain when depressed in inspiration, but, if on returning to their position against the body wall they relaxed their hold, the grain is shot backwards over the carapace. Sometimes the grain is caught in the expiratory stream from the pseudorostral chamber as it is shot backwards and then it passes forward in front of the animal with great force. Once collected the food is passed to the mouth parts, probably along a ventral food stream. There is no positive evidence of the existence of this food stream, but it is believed that some of the water about to pass into the respiratory funnel escapes and passes along the depression leading to the mouth, carrying with it the food scraped off the grains by the maxillipedes. The maxillae and maxillules pick up the food particles from the stream and pass them on to the mandibles to be masticated before entering the mouth. *Cumopsis* resumes feeding whenever it contacts food, while resting on the surface of the substratum, or in the initial stages of burrowing. However, certain rapid movements of the soil particles around the anterior end of the cephalothorax when the animal burrows into the soil are due to the close proximity of the grains to the expiratory stream, and not to feeding.

All the food-collecting limbs are well armed, and the function of the armature depends upon its nature and position on the respective limbs. The first peraeopod has on its dactylus four long bristles which can be spread out fan-wise to feel the substratum. These bristles have stout axes, and are slightly bent distally where they carry short combs made up of close-fitting teeth (Fig. 4). These bristles are probably tactile organs capable of locating the food, as well as being fine grasping organs. The dactylus and propodus of the third maxillipede carry bristles with short axes, which possess either one or two ventrally placed combs along their entire length. The teeth of the combs are triangular in shape and have sharp extremities (Fig. 4). These are fine grasping organs, and in this purpose they are assisted by the slightly twisted nature of the dactylus. A smaller version of the same bristle occurs on the propodus and carpus of the second maxillipede, which is used to scrape the grain in the cleaning process. Further assistance in cleaning the grain is given by the feathered bristles on the inner edges of the merus of the second maxillipede, and by the strong, smooth and sharp bristles on the inner edges of the merus and carpus of the first maxillipede (Fig. 4). These last two types line the hollow into which the grain is placed by the third maxillipedes. The maxilla comb is composed of smooth setae which lack the fine delicate setules described by Dennell for Diastylis bradyi, and this makes their value as a filter mechanism doubtful.

BURROWING AND SWIMMING

The Cumacea burrow into the substratum if the soil grade is favourable. Zimmer describes how *Diastylis rathkei* refuses to burrow into sand, and in this investigation it was found that *Cumopsis* would not burrow into mud. The last four pairs of peraeopods are used in burrowing. The burrowing movements were observed by placing the animals in a dish of sea water with a few scattered sand grains to act as a stimulus. At rest the burrowing peraeopods lie close together on the ventral side of the body. Burrowing activity begins with the separation of these peraeopods in such a way that the animal appears to be standing on them, with its body lifted from the ground. This is immediately followed by a simultaneous movement of all the peraeopods. The second pair move forward and backward in an anterior to posterior direction,

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and the three subsequent pairs move outward and inward in a lateral direction. In this way sand is scooped away from underneath the body and the animal sinks into the hollow thus formed. The posterior region of the thorax and the

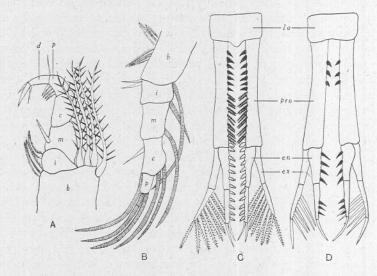


Fig. 5. A. Feathered bristles on the basis of the 3rd maxillipede. B. 2nd peraeopod. C. Uropods of male. D. Uropods of female. *en*, endopod; *ex*, exopod; *la*, last abdominal segment; *pro*, protopod. Other lettering as in Fig. 4.

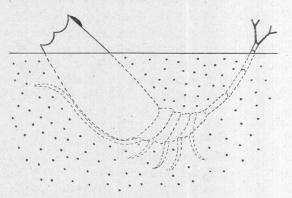


Fig. 6. Diagram to show the position of C. goodsiri in the soil after burrowing.

anterior region of the abdomen are buried first. The sand which has been shovelled away becomes banked up on either side of the body and after a time collapses on top of the animal. By pushing its body backwards under this cover of sand it attains almost complete burial. A part of the pseudorostrum remains exposed at one end of the tunnel, and the uropods at the opposite end (Fig. 6). In *C. goodsiri* the last three pairs of peraeopods have a very decided curved shape, which is further emphasized by the presence of long, curved and ridged bristles (Fig. 5B). These help to scoop away the sand grains.

Though predominantly a burrower Cumopsis can swim actively as well. This swimming ability is made full use of in the moonlight swarms in which they are known to participate. In swimming, use is made of the exopodites of the first peraeopods and the abdomen, but both function independently. Thus the animal can swim by flexing the abdomen. The latter is brought forward underneath the cephalothorax and then violently flexed back into position. Quick repetition of this method and the consequent compression and release of water involved, pushes the animal forward in a rapid jerky manner. At other times it swims by rotating the exopodites of the first peraeopods and this is a fast even method of locomotion. In C. goodsiri only the exopodites of the first peraeopods are used in swimming. Foxon (1936) describes the use of the exopodites of the first peraeopods and the third maxillipedes in Lamprops fasciata. But a dissection of Cumopsis showed how the exopodites of the third maxillipedes lie wedged in between the bases of the maxillipedes and the body wall and are therefore incapable of the free movement necessary in swimming. Fully developed males also possess five pairs of pleopods on the abdomen which are sometimes used in swimming. During the investigation they were only seen to be used when the exopodites of the first peraeopods were removed. The principal methods of swimming in both adult and young stages of male and female specimens are by flexures of the abdomen and by rotation of the exopodites of the first peraeopods.

CLEANING OF THE BODY

Cumopsis uses the uropods which are found at the end of the abdomen to clean away detritus or any other matter that may become attached to the surface of the body. The abdomen is brought forward beneath the cephalothorax, to lie near the particular part of the body in need of cleaning (Fig. 7A). Sometimes the uropods diverge on either side of the carapace (Fig. 7B). Once the uropods have taken up their position, the abdomen is drawn backward and forward, and the uropods scrape away any material adhering to the body. Each uropod consists of a protopod, an inner endopod and an outer exopod (Fig. 5 C, D). They are usually well armed, but the armature is subject to ontogenetic and sexual differences. It is best developed in the adult male and consists of smooth spines, comb-spines, comb-bristles and delicate feathered setae. The general surface of the whole uropod is rough on account of the minutely serrated character of the chitinous exoskeleton. This rough surface together with the spines and bristles scrape away the depositions on the body. The feathered setae which are found on the exopods of the male may act as filters to catch the material scraped off by the uropods, and which is later washed away in swimming. But it is possible that they have the more active function of brushing away the material loosened by the endopods. The uropod

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is extremely flexible, and this flexibility is the result of an efficient joint arrangement between the segments. The junction between the protopod and last abdominal segment appears to be of the hinge-joint type, allowing only for a bending movement in the ventral direction. A similar hinge joint exists between the protopod and the endopod. But the junction between exopod and protopod is marked by a characteristic bulge, and this seems to indicate a balland-socket joint capable of considerable flexibility.

The uropods of the female and young male are always less heavily armed than those of the adult male. Since at all stages in the life history subsequent to leaving the brood pouch, the animal is constantly exposed to detritus and therefore in need of efficient cleaning organs, it would be expected that the

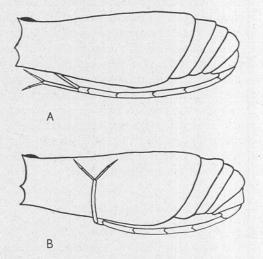


Fig. 7. Diagram of the different positions taken by the uropods during cleaning movements.

most important features of the cleaning apparatus would be present throughout ontogeny in the individuals of both sexes. In *Cumopsis* these include the general rough surface and flexibility of the uropods. The armature seems to be a later development which becomes fully developed at maturity and adds to the efficiency of the cleaning movements. Why the adult male should have uropods more heavily armed than the female is difficult to understand. The male uses the protopod combs to clean its long antennae, and the absence in the female of a counterpart to these long antennae may account for the lack of protopod combs to some extent, but these combs help to clean other parts of the body as well. From the functional standpoint the uropods should be equally armed in both sexes. It may be that the adult male shows this greater development of armature because it favours localities in the habitat which are richer in their detritus content. There is no direct evidence of this assumption, but the difficulty, when collecting, of finding adult males and females to-

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gether seems to lend support to the idea. Adult females and young males are frequently collected from the same patch of soil, but adult males seem to inhabit patches of soil on their own.

SUMMARY

The breathing, feeding, swimming, burrowing and cleaning habits of Cumopsis goodsiri are discussed.

Cumopsis has compact respiratory chambers. The inspiratory current enters each gill chamber posteriorly at the base of the third maxillipede, and the expiratory current leaves anteriorly through the siphons which pass through the pseudorostral chamber. The inspiratory current is filtered from all suspended particles by a sieve placed at the mouth of the respiratory funnel. which is formed by the depression of the third maxillipede away from the body. The size of the spaces in the mesh of this sieve probably determines the grade of the substratum in which the animal can live.

Cumopsis feeds on micro-organisms which it cleans off sand grains and other small objects. These are collected by the first peraeopods, held in position by the third maxillipedes, and cleaned by the first and second maxillipedes. The food is then passed on to the maxillae, maxillules and mandibles and finally enters the mouth. All these appendages are suitably armed to perform their respective functions.

Use is made of the last four pairs of peraeopods in burrowing and Cumopsis will only burrow into a sandy substratum. Swimming is accomplished in three different ways: (a) by flexures of the abdomen, (b) by paddle-like movements of the exopodite of the first peraeopod, and (c) in adult males by the abdominal pleopods.

The body is cleaned by the uropods. Their general rough surface and flexibility is very important. The uropod armature seems to add efficiency to the cleaning movements in the adult animals, particularly in the males.

The size of the soil particle is vitally important in the distribution of the Cumacea. It determines whether the animals breathe properly. There is also probably a close association between the soil grade and distribution of soil micro-organisms upon which they feed. As a result they refuse to burrow into a soil grade which is unfavourable.

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