Contributions to Marine Bionomics.

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I. The Habits and Respiratory Mechanism of Corystes cassivelaunus.

Corystes cassivelaunus is a crab of unusually narrow and elongated form, which has received the popular name of "masked crab" from the grotesque resemblance which its sculptured carapace bears to a human face. It is common round all the coasts of the British Isles, and, although normally an inhabitant of the deeper water, is occasionally found at home in sandy pools on the sea shore, and is frequently cast up in hundreds on sandy shores after heavy gales.

I. Systematic Position.

The systematic position of the Corystoidea has long been a disputed point among carcinologists. Henri M. Edwards (1834) placed the Corystoid crabs near the Dorippidæ among the Oxystomata, and regarded them as connecting links between the Cancroidea (*viâ* the Calappidæ) on the one hand, and the Anomoura on the other.

De Haan (1849) removed the family from the group Oxystomata altogether, and placed it with the Cyclometopa and Catometopa of M. Edwards, in a separate sub-division of the Brachyura, the Brachygnatha.

Dana (1852) made of the Corystoidea an independent and primary tribe of the Brachyura, distinct from the Cancroidea and Leucosoidea alike.

Alphonse Milne-Edwards (1860) reverted to the older view, and placed the Corystidæ near the Calappoid Oxystomata. Heller also (1863) placed the Corystidæ among the Oxystomata.

Finally, Claus (1880) definitely placed the Corystidæ in the Cyclometopa. In this he has been followed by Miers (1886) and Stebbing (1893).

It cannot be said, however, that the real position and affinities of the Corystidæ are yet established. The reason for this uncertainty is probably due to the fact that, as will appear further on, the structure of these animals is remarkably modified in relation to sand-burrowing habits. Some of these adaptive modifications of structure, which reappear in certain other groups of Crustacea, have undoubtedly impressed the minds of certain writers with ideas of homology and genetic relationship between the Corystidæ and groups having no real affinity with that family. The case affords a new illustration of the inadequacy of the purely morphographic method, when unchecked by considerations of functional adaptation, for the solution of problems of relationship and genetic classification.

II. Structural Peculiarities.

The structure of *Corystes cassivelaunus* is noteworthy on account of the following features. The second antennæ are greatly elongated—as long as, or longer than, the body—and are fringed along their entire length by two rows of hairs, one of which runs along the ventral, while the other runs along the dorsal border of the antenna. The hairs of each row curve inwards towards those of the corresponding row on the second antenna of the opposite side. The second antennæ shew a marked tendency to approximate to one another longitudinally; the opposing rows of hairs then interlock, with the resulting formation of a median tube, the lateral walls of which are formed by the jointed flagella of the antennæ, while the dorsal and ventral walls are fenestrated along their whole extent by the interspaces between the interlocking hairs. The organ formed by the apposition of the second antennæ I shall term the "antennal tube."

The long axes of the three stout basal joints of the second antenna are disposed at right angles to one another, and bring about a characteristic double bend in the basal part of the antenna. The double row of hairs found on the flagellum of the antenna is continued backwards along these three basal joints. The hairs on the most distal of the three joints interlock with those of the corresponding joint of the opposite antenna; the hairs on the anterior face of the deflected middle joints bend inwards towards the median line along the sides of the rostrum, and together with a median triangular tuft of hairs springing from the rostrum itself, form the hairy roof of the proximal part of the antennal tube.

The antennal tube opens posteriorly into a rectangular chamber in front of the mouth. This "prostomial chamber," as it may be termed, is roofed by the rostrum in front, the antennal and epistomial sternites in the middle, and the prelabial plate behind. It is flanked by the two basal joints of the second antennæ in front, and by a forward process of the pterygostomial region of the carapace behind. Its floor is imperfect, and is formed by the anterior part of the third maxillipeds behind, and by a quadrangular sieve in front, furnished by the hairs springing from the two basal joints of the second antennæ, the anterior pterygostomial processes, and a special anterior process of the fourth joint of the external maxillipeds. The hairs from all these parts are directed inwards towards the centre of the quadrangular space outlined by the boundaries of the prostomial chamber, and constitute a complete sieve-like floor to the chamber in question. On each side this prostomial chamber leads by a wide aperture into the branchial cavity.

The participation of the epistome together with the prelabial space in the formation of a prostomial chamber is one of the features which strongly distinguishes the Corystoid crabs from typical Cyclometopa, Catometopa, and Oxyrhyncha. The arrangements of these parts approximates in some respects to that found in the Oxystomata, where the buccal frame or the peristome is prolonged anteriorly as a definite prostomial chamber to the very tip of the snout. This chamber in the Oxystomata, however, is completely closed in by the third maxillipeds, and is very narrow anteriorly; in the Corystoidea, on the other hand, it is broad in front, and is imperfectly closed by the third maxillipeds.

III. Previous Observations on Habits.

In Bell's "British Stalk-Eyed Crustacea" (1853) a brief reference is made to the sand-burrowing habits of *Corystes cassivelaunus.* Couch had already described the crab as "burrowing in the sand, leaving the extremities of its antennæ alone projecting above the surface." The actual process of burrowing appears not to have been observed at the time when Bell wrote, for he quotes Couch's suggestion that the elongated antennæ possibly "assist in the process of excavation." This theory of the function of the antennæ was subsequently rejected by Gosse (1865), as a result of his own observations on the habits of the crab, and again by Hunt (1885), who correctly states that the crab descends into the sand backwards with the greatest agility, "thus leaving the antennæ no opportunity of assisting in the operation."

The first writers to offer anything approaching a real explanation of the use of the antennæ were the veteran naturalist of Cumbrae, Mr. David Robertson, and Mr. P. H. Gosse. It is difficult to say, and would indeed be ungenerous to enquire, which of these two naturalists has the priority in the matter. Gosse, in 1855, described the outer antennæ of *Corystes* as "together forming a tube" (*Manual of Marine*

Zoology, I., p. 158), but he did not apparently publish his observations in full until 1865.

In the meantime Mr. David Robertson communicated to the Philosophical Society of Glasgow, on March 13th, 1861, an interesting note on the function of these antennæ. He described the burrowing habits of the crab, and shewed that, under these circumstances, the antennal tube preserved "a free passage for the purpose of enabling the animal to carry on the process of its aqueous respiration." Mr. Robertson believed, with Gosse, that the current through the tube was exhalent in character. In another paper he stated that "he had seen the ova cast up through the opening [of the antennal tube]—the inference being that the animal had placed it by means of its claws within the influence of the current." (*Proc. Nat. Hist. Soc., Glasgow*, vol. i. p. 1.)

Gosse (1865) similarly observed that each antenna, from the form and arrangement of its bristles, constituted a "semi-tube, so that when the pair was brought face to face the tube was complete." He also carefully watched a living specimen, as it was sitting upright on the top of the sand, close to the side of a glass aquarium, and observed that the antennal tube formed a channel for a definite current of water. To quote his own words: "I immediately saw that a strong current of water was continuously pouring up from the points of the approximated antennæ. Tracing this to its origin, it became evident that it was produced by the rapid vibration of the foot-jaws, drawing in the surrounding water, and pouring it off upwards between the united antennæ, as through a long tube. . . ." "I think, then, that we may, with an approach to certainty, conclude that the long antennæ are intended to keep a passage open through the sand, from the bottom of the burrow to the superincumbent water, rendered effete by having bathed the gills; and it is one of those exquisite contrivances and appropriations of structure to habit which are so constantly exciting our admiration . . . [and] are ever rewarding the research of the patient observer."

We shall see below that while Gosse's conduit-theory of the function of the antennæ is perfectly correct, his inferences as to the function of the antennal conduit are true only to a limited extent. Gosse assumed that the habits of the crab when beneath the sand were similar to its habits when above the sand, and confined his observations to the crab in the latter condition. Experiment shews, however, that there may be a marked difference in the working of certain organs under the different conditions.

A third theory as to the function of the antennæ in *Corystes cassivelaunus* is due to Mr. A. R. Hunt (1885). He says, "I incline to think that the function of the antennæ is to maintain a communication between the buried crab and the water above, as without some such connexion there would be a risk of the animals being occasionally buried to a dangerous depth by the accumulation of sand above them. Mr. W. Thompson's statement that the antennæ in very small specimens are much longer in proportion to the carapace than in the adult harmonizes well with this hypothesis, as to ensure safety the young would have to burrow to a greater depth compared with the adults than would be proportionate to their size." Mr. Hunt was not aware of Gosse's view when he framed the above theory; but, subsequently, in a footnote to his paper, he referred to Gosse's theory as identical with his own. The two are, however, essentially distinct, if I correctly understand Mr. Hunt's language. According to Gosse's view, the function of the antennæ is to produce a tube subservient to respiration; according to Mr. Hunt's, the function of the elongated antennæ is essentially sensory, viz., to enable the buried crab to determine the depth to which it burrows. The "danger" to which Mr. Hunt refers is clearly not the danger of suffocation, but the danger of dislodgment from the sand by wave-currents. The arenicolous habits of *Corystes* are adduced by Mr. Hunt to illustrate one of the various methods adopted by marine animals for resisting wave currents—a view which, in the case of *Corystes,* I am unable to accept, partly on account of the normally deep water habitat of the crab, and partly on account of evidence given below which tends to shew that the burrowing habits of *Corystes* are adopted primarily for concealment.

IV. New Observations and Experiments.

(a) Burrowing Habits. A number of living *Corystes cassivelaunus* were placed in a series of vessels containing sand of different degrees of coarseness, and it was soon noticeable that these crabs readily burrow in fine sand, but find great difficulty in penetrating very coarse sand or gravel composed of small pebbles. Moreover, a crab that has obstinately declined for several hours to burrow in coarse, gravelly sand, will immediately bury itself, if placed in an aquarium of fine sand. In all cases the process of burrowing is effected exclusively by means of the thoracic legs. The crab sits upright on the surface of the sand; the elongated, talon-like claws of the four hindmost pairs of legs dig deeply into the sand; the body of the crab is thus forcibly pulled downwards by the grip of the legs, and the displaced sand is forced upwards on the ventral side of the body by the successive diggings and scoopings of the legs; the slender chelate arms of the first thoracic pair assist in the process of excavation by thrusting outwards the sand which accumulates round the buccal region of the descending crab. This action at the same time, no doubt, loosens the sand in the immediate neighbourhood, and

renders easier and quicker the descent of the crab into its sandy burrow. Briefly stated, in fact, the four hindmost pairs of legs are all engaged in pulling the crab downwards, while the first or chelate pair is engaged in pushing away the more superficial sand in the neighbourhood of the crab's maxillipeds. The two actions combine to drive the crab downwards and obliquely backwards. The main object of this latter motion appears to be the prevention of any forcible intrusion of sand into the buccal apparatus.

When the carapace of the crab has completely disappeared beneath the surface of the sand, the antennæ are frequently seen to be rubbed obliquely against one another for two or three strokes, whereby the hairs on the antennæ are cleansed from adhering particles. This very characteristic action of the antennæ was noticed long ago by Couch, and correctly recognised by him as a process of cleansing (*vide* Bell, p. 161). After this cleansing process, however, the crab proceeds still further in its act of burrowing, and descends deeper and deeper until nothing is visible above the sand but the most distal portion of the antennal tube.

Resting passively in its bed of sand, *Corystes cassivelaunus* spends the daytime thus concealed from all observation. In aquaria an individual will occasionally emerge and remain on the surface of the sand for some time, but this can usually be attributed to the restlessness resulting from strange conditions. I am inclined to think that if the water and sand provided be of a perfectly suitable character, *Corystes* will remain imbedded throughout the day. (cf. Robertson, l. c. *supra*).

I have noticed, however, that individuals which were inactive and concealed beneath the sand during the day, shewed a marked tendency to activity at night. I have observed on several occasions that my aquarium, containing some half-dozen of these crabs, was the scene of distinct excitement and activity late at night; the crabs had emerged from the sand, and were restlessly hobbling about on the surface, as though in search of food. Although I cannot make a final statement upon the point, all my experiences incline me to the view that *Corystes cassivelaunus* is a nocturnal animal; it conceals itself in the sand by day as a protection from sight-feeding fishes, but emerges at night for food and recreation. If these habits were absolutely constant, we should expect to find the eyes of *Corystes* undergoing retrogressive changes, as, for example, in the case of *Pinnotheres.* Such is not the case, however, for the eyes are capable of forming distinct images, as well as, no doubt, of distinguishing light from darkness.

(b) Respiratory Currents. We have seen that Gosse observed a current of water setting upwards from the buccal region of the crab

through the antennal tube, and carrying upwards the water which had previously bathed the gills. This current was caused, according to Gosse, by the "vigorous vibration of the foot-jaws." The crab observed by Gosse was sitting on the top of the sand—not beneath it.

If some sea-water be coloured by the addition of a little Chinese ink, or finely powdered carmine (the former is the better material), and if a few drops of the coloured water be added to the water in the neighbourhood of the antennal tube of a buried crab, it will invariably be found that the current which sets through the antennal tube is from above downwards, and not *vice versa*. The same current may often, and indeed generally, be shewn to exist, even when the crab is not imbedded in the sand.

It will then be noticed that the coloured water is sucked between the hairs of the antennal tube, and passes downwards and backwards to the prostomial chamber. Here, in front of the labium, the current divides into two streams, one right and one left, which pass outwards and backwards into the right and left branchial chambers respectively. Finally, the coloured stream emerges from the branchial chamber beneath the edge of the branchiostegite, not at any one point, situated either anteriorly or posteriorly, but along its whole extent, and especially between the bases of the legs.

The direction of this current through the branchial chamber is the reverse of that which has hitherto been recognised in all other Decapod Crustacea. In these (*e.g.*, *Maia*, *Cancer*, *Carcinus*, *Astacus*) the current which bathes the gills is known to enter this chamber beneath the branchiostegite, and to emerge in front by the lateral aperture at the side of the mouth. The normal peribranchial current in Decapod Crustacea is from behind forwards; I shall, therefore, term the current of the buried *Corystes* a "reversed current," and shall speak of the whole phenomenon as a "reversal" of the normal current.

Although *Corystes cassivelaunus* constantly exhibits this reversed current when imbedded in the sand, yet it is occasionally possible to observe the normal current in the same specimen when the animal is not buried. The coloured water is then rejected when added near the antennal tube; but if deposited near the bases of the legs, is sucked inwards, and eventually emerges from the branchial cavity into the prostomial chamber, and thence passes either directly to the exterior or forwards by way of the antennal tube. When the normal current is at work it frequently happens that the exopoditic palps of the maxillipeds begin to vibrate. The action of these palps still further intensifies the force of the exhalent currents, and at the same time disperses the streams of water laterally, *i.e.*, the water, instead of passing to the exterior anteriorly in an even stream, is partially diverted to the sides of the crab's body, and is scattered outwards and laterally by the vigorous lashings of the exopoditic palps.

Gosse's observations on the respiratory currents of *Corystes cassivelaunus* are thus seen to be incomplete rather than inaccurate. A current *may* be directed outwards through the antennal tube, and the effete water from the branchial chamber *may* be carried away by that channel; but such a direction of the current in *Corystes cassivelaunus* is not constant, as Gosse believed, or even usual. Moreover, when the crab is imbedded in sand, the current is always reversed, except for a few seconds now and then, when the crab desires to eject distasteful particles which have entered the prostomial chamber with the respiratory current. Under such circumstances the reversed inhalent current through the antennal tube is temporarily replaced by a forcible exhalent current. But as soon as the desired ejection has been effected, the reversed current is again set up. This voluntary inhibition of the reversed current can be easily demonstrated by the addition of carmine to the water setting through the antennæ. Oddly enough, a weak solution of Chinese ink is less distasteful to *Corystes* than a mixture of powdered carmine and sea-water.

(c) Cause of the Currents. The direction of the respiratory currents is exclusively due to the movements of the scaphognathite, the valve-like and highly muscular appendage of the second maxilla, which is known to produce the regular respiratory currents of other Decapoda. H. Milne-Edwards first demonstrated the important *rôle* played by the scaphognathite in Decapod Crustacea; and he maintained that the direction of the respiratory current was absolutely constant, *i.e.*, from behind forwards in all Decapods (1839, p. 136). De Haan (1850, p. 117) has indeed suggested that the current to the branchiæ passes from before backwards; but his remarks on this subject are obviously the result of mere inference, and are not determined by actual experiment. He states, for example, that in *Portunus* the inhalent current sets inwards not only through the aperture between the base of the cheliped and the edge of the branchiostegite, but also through the anterior aperture at the side of the mouth. Experiments on *Portunus* have shewn me that this is quite devoid of foundation; the water certainly enters—in part—through the former of these apertures, but the aperture at the side of the mouth is invariably exhalent in function.

In the case of *Corystes* I observed the action of the scaphognathite by removing the three maxillipeds and the edge of the pterygostomial fold of a living specimen. The scaphognathite was completely exposed by this preparation, and its movements were readily followed.

When the normal current—from behind forwards—was at work, the propulsion of the water could be seen to be effected by a sharp, prompt blow dealt by the posterior lobe of the scaphognathite, which was succeeded by an undulatory movement from behind forwards of the remaining part of the scaphognathite. As the crab lay on its back the anterior lobe could finally be seen to descend slowly and gently upon the anterior edge of the roof of the chamber, gliding along, and, as it were, stroking its polished surface.

When the current is reversed, however, the action of the anterior lobe is quite different; it strikes the water in front with a prompt, decisive blow, and this is succeeded by an undulatory movement of the rest of the scaphognathite from before backwards. The water lying between the valve and the roof of the chamber is thus driven backwards into the branchial cavity. The action of the scaphognathite is fairly rapid, but after a little observation, checked by the employment of coloured water to test the currents, it becomes quite easy to detect with certainty the direction of the current by inference from the movements of the scaphognathite alone.

The action of the exopoditic palps of the maxillipeds in causing currents has already been described. Such currents are purely accessory, and Gosse (1865, p. 130) and De Haan (1850, p. 117) have undoubtedly erred in assigning to the maxillipeds an important share in the production of respiratory currents.

V. Evolutional Significance.

The habits of *Corystes cassivelaunus* described above seem to me to demonstrate the adaptive nature of the entire organization of this Crustacean, and slight consideration is all that is required to enable a naturalist to recognise the utility of these adaptive features.

The burrowing habit is useful as a mode of concealment from enemies. The elongation and smoothness of the carapace, and the elongated claws of the four hindmost pair of thoracic legs, are all features usefully correlated with the specialization of the crab for a sand-burrowing existence.

The elongation of the antennæ and the arrangement of the hairs upon them, the double bend of their basal joints, the structure of the parts bounding the prostomial chamber, and the arrangement of hairs upon them, are characters which, in conjunction with the reversal of the respiratory current, adapt the respiratory mechanism of the crab in a remarkably complete manner to an arenicolous mode of life. The antennal tube enables the crab to draw its supplies of water directly from the superincumbent reservoir of water, while the arrangement of hairs is such as to constitute a sieve, keeping the sand away from the respiratory organs.

The upright position of the crab is itself a most unusual feature, and is correlated with the formation of an elongated antennal tube; the posterior position of the legs is functionally correlated with the adoption of the upright attitude.

VI. Analogies.

A reversal of the respiratory current similar to that which I have just described in *Corystes* also takes place under certain conditions in the allied form *Atelecyclus heterodon.* The habits of this crab are much more complex than those of *Corystes,* and will form the subject of a later article.

An elongation of the antennæ, and their conversion into an antennal tube by the interlocking of hairs along their margins, also takes place, as I have recently discovered, in an East Indian Crustacean, *Albunea symnista,* Fabr., which belongs to the Hippinea among the Macrura Anomala (Anomura). In this type, however, the antennal tube is formed by the first and not by the second pair of antennæ. The antennal tube has obviously been produced independently in *Corystes* and *Albunea,* and affords a remarkable example of homoplastic modification. In all probability the function of the tube is the same in both cases, but no direct observations on this head in the case of *Albunea* have yet been made.

It seems to me not unlikely that further observation of the habits of *Hippa talpoida* of the American coasts will reveal an essentially similar sieve-like function for the curiously bent and setose second antennæ of that animal.

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