Notes on the Œcology of *Cirratulus* (*Audouinia*) *tentaculatus* (Montagu).

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With Figures 1 to 7 in the Text.

Cirratulus tentaculatus is found inhabiting the wet, sandy, somewhat foul mud of the Aberystwyth shore, chiefly in the Laminarian zone, although it also occurs in rock pools higher up the shore in which there is sufficient depth of sand containing the necessary organic matter. The presence of the worm in its natural habitat is indicated by a group of delicate, elongate, rosy or yellow coloured filaments of tentacular appearance which protrude from the sand into the pools left by the receding tide. These filaments nearly always display a certain amount of movement, either waving gently from side to side or curling slightly from the tips. The amount of motion and also the colour of the filaments will depend on the degree of freshness of the water in the pool, and this, of course, will, in its turn, be related to the state of the tide.

Specimens are not easy to collect owing to the marked propensity the animal exhibits for lying with its body beneath stones or pieces of rock embedded in the mud. In rock pools or crevices where there is but little depth of sand and the animal lies with its body more or less parallel to the surface collection is almost impossible. This response to stimuli of contact and pressure, or, as M. Georges Bohn has it, this "thygmotactism," is very marked, and, in the aquarium, when specimens are placed in a vessel containing sand and a few stones, the animals will roam about till some portion, at any rate, of their bodies is undergoing pressure from those stones.

Thus, in addition to the occurrence of sandy mud of rich organic content, the worm would seem to require the presence of a certain amount of rock or loose stones. Both these requirements are well met on the portion of the Aberystwyth shore opposite the College. Here a large reef of rock runs out to sea in such a manner as to form a barrier to the prevailing wind and thus to aid in the deposition of organic matter, of which no doubt a certain proportion is contributed by the Harbour sewer lying to southward, decaying fragments of algæ, etc.

When withdrawn from the mud Cirratulus presents an exceedingly limp and bedraggled appearance. The body appears to possess, when in this partially extended condition, absolutely no turgidity. This is in agreement with the animal's marked thygmotactism, the necessary tension being secured in the natural habitat by the pressure of stones.

A detailed account of the external characters is no longer necessary, owing to the recent appearance of Vol. 3 of Prof. McIntosh's memoir on British Marine Annelids, containing the Cirratulidæ (1). It is sufficient to say that the species *tentaculatus* is distinguished by the occurrence of lateral filaments on segments anterior to the fifth chætigerous segment behind which the paired fascicles of filaments arise.

Considerable doubt seems to exist as to the analogy of the lateral filaments with those of the paired tufts. Prof. McIntosh quotes Claparède as distinguishing (in *C. chrysoderma*) between tentacles and branchiæ in such forms by the fact that the former have only one blood-vessel, whilst the latter have two. In *Audouinia filigera*, on the contrary, every filament is branchial in structure. De St. Joseph (2) distinguishes between Cirratulus, in which the tentacles appear at the same time as the branchiæ, and Audouinia, in which the segments bearing the tentacles are preceded by a variable number of segments with lateral branchiæ, and remarks that in neither case do the tentacular filaments and lateral branchiæ differ materially in external appearance. Cunningham and Ramage (3), on the other hand, describe a groove along the so-called tentacles and find it to contain only a single blood-vessel, whereas in the branchiæ two blood-vessels are present.

J. Bounhiol (4), in an ingenious paper on Respiration in Polychætes, denies any respiratory function to either kind of filaments; he says if a specimen of either *Cirratulus cirratus* or *C. tentaculatus* be placed in a glass vessel the floor of which is covered with sand, the animal is soon seen to make active use of the tentacular filaments to remove the sand grains, draw them towards itself and more or less cover itself with them. These filaments have been placed by anatomists in two categories, according to whether they contain a simple vascular cæcum or a complete vascular circuit. The first are called tentacular filaments, the others gills. But the animal uses both kinds indiscriminately as prehensile organs. It has also been shown by experiment that the respiratory rôle of these so-called gills is very feeble, and merely corresponds to an increase of the body surface. "La définition anatomique des branchies de Cirratulidæ n'est donc pas confirmée par l'expérimentation physiologique. Ce sont de simples organes prehensiles, tout comme les filaments prehensiles dont on avait cru pouvoir les distinguer."

The experiments of M. Bounhiol on Cirratulus in his examination of the filaments as respiratory organs were faulty as they made no allowance for the animal's natural habitat. The rôle played by the filaments is essentially respiratory; further, close observation has shown that the prehensile function, so readily admitted by most authors, is non-existent. Careful study of the animal's habits shows that there is absolutely no need for such a function, whereas there is every need for that of respiration. What leads the majority of observers to suppose a prehensile function is undoubtedly the perpetual curling motion of the filaments in the pools. A differentiation of function between the lateral filaments and those in the paired fascicles is undoubtedly suggested by their behaviour when the animal is withdrawn from the mud. The filaments in the clusters immediately contract, their colour becoming quite yellow, while the remaining lateral filaments are still more or less distended by the contained blood, and are, of course, red in colour. These superficial differences, however, do not necessarily prove any difference in function, and this notwithstanding the disparity in structure referred to by Bounhiol. [It has been suggested that the fascicles of filaments are prostomial tentacles which have shifted backwards, Meyer (12)]. The worm is essentially and in all except perfectly abnormal conditions a burrower, and consequently permanently subject to pressure. When all pressure is relaxed and the animal bathed on all sides by water it is only natural that, with respiration taking place over the whole body surface, numbers of filaments should be left idle, and it would be particularly the filaments lying in front of the heart-body which would be affected. In further response to the relieved pressure the animal contracts and curls up, the anterior part of the body is forced beneath the coils and the prostomium is protruded as far as possible, and the characteristic actions of burrowing are performed, that is to say, the anterior region is pumped turgid with fluid and waves of muscular contraction pass along the body from behind forwards. At the same time the mucous investment, with the sand adhering from the burrow, is gradually shed and becomes caught in the gill filaments, and an inextricable tangle is the result. Prof. McIntosh notes that the animal appears to be less comfortable in pure sea water, and thinks the mud to be the most fitting medium, since it keeps the filaments apart. Undoubtedly, mud is a more fitting medium, but not, I think, for this latter reason. If a number of flat stones be laid upon the bottom of the vessel, the worm, a few hours later, will be found ensconced beneath them and numbers of filaments will stretch in all directions, without any trace of entanglement, showing that what the animal chiefly lacks is pressure.

The appearance of the gill filaments when the worm is in its natural habitat is sufficiently familiar, but the manner in which they attained that position, in view of their extreme delicacy, is rather remarkable. If the worm be withdrawn from the mud on the floor of the pool and left on the surface, it will immediately coil up and commence to burrow again in the manner already noticed. Owing to the downward and forward movement the gill filaments will tend to stream backwards, and, as the worm progresses, being extremely elastic, their distal portions will remain at the surface, the filaments stretching till the animal has found its proper level. The portions of the filaments remaining in contact with the water will thus be available for aeration of the contained blood.

The question now arises as to how the animal would react should the filaments become buried beneath several inches of mud, as must often happen.

In order to answer this question a specimen of Cirratulus was placed at the bottom of a glass vessel 5 inches high by $2\frac{1}{4}$ inches in diameter, covered with mud to the height of two inches, and the remainder of the vessel filled with water. Four hours later a number of filaments were projecting at the surface. The following day, when about 20–30 filaments were projecting, another $2\frac{1}{2}$ inches of mud were added. Two hours later one filament had been protruded. This time, by a lucky chance, the anterior end of the worm was in contact with the glass close to the top of the first layer of mud, and its behaviour could thus be observed. The body of the worm itself was practically stationary, some of the filaments of the anterior fascicles were yellow and motionless, but numbers which were gorged with blood showed remarkable activity, and were gradually yet speedily forcing their way upward through sand and mud to the surface, exactly as if they were so many individual worms. The extensility and muscular activity of the filaments is therefore enormous, the length of some of them from their junction with the body wall to the tips exceeding three inches.

The whole forms a remarkable adaptation to an underground habitat. The majority of species of Polychætes inhabiting the same environment are either of small size and able to respire through the body wall generally, or they are obliged to mount to the surface to avoid asphyxiation. Cirratulus is able to live permanently surrounded by the sandy mud where it finds its food supply (reference to which will be made later), and by remaining constantly underground is well protected from enemies. The large numbers in which Cirratulus occurs is sufficient proof of its success.

We have seen that when the body of the worm is undergoing pressure the filaments are stimulated to great activity by the pressure of blood in their vessels, and on seeking an explanation of this phenomenon, we cannot help being struck by the fact that in the Cirratulidæ, the heart-body, the function of which has aroused so much curiosity, reaches its greatest development.

The structure and function of the heart-body, in this and in other groups where it occurs, has been discussed by L. J. Picton (5) and, several years previously, by J. T. Cunningham (6). Although the former writer is chiefly concerned with the composition of the granules contained in the cells forming the body, and of their reaction to various stains, his object being principally to examine its claims as an excretory or blood-controlling organ, he nevertheless gives a certain amount of attention to its possible mechanical function. He quotes the suggestion of Schaeppi (7) in the case of Ophelia and of Steen in that of *Terebellides Stroemii* to the effect that the organ has a valvular function. Schaeppi considers this is brought about by the swelling of the organ at systole owing to the pressure of blood in its meshes. The most telling evidence in favour of a mechanical action is that afforded by *Cirratulus chrysoderma*. Picton says that in this species, which is transparent, the heart-body at the point of its greatest development almost entirely blocks, at systole, the lumen of the heart, the action of which as a blood-propelling organ must be considerably modified.

It seems certain from what has been noted of the habits of Cirratulus that it depends to a great extent amid its somewhat foul surroundings, for its supply of oxygen, on the long filaments. There is, therefore, every necessity, in view of their delicate nature, for maintaining them turgid. Otherwise, they would be extremely liable to breakage and laceration. This difficulty would be met by the heart-body acting as a valve and preventing the blood from being regurgitated. It is certainly remarkable that in Arenicola, to which genus the above arguments apply with almost equal force, the heart-body is also strongly developed. J. H. Ashworth (8) also suggests a valvular function in this latter, and the fact that the organ does not appear till after the pelagic larval and post-larval stages are complete is not without significance. Some such arrangement would be a small compensation for the drawbacks to which Arenicola, with its delicate branched gills, must undoubtedly be exposed, through its sandy environment.

External processes with respiratory properties are a common feature in Polychætes, but that does not necessarily imply the same need for a heart-body, with the function described, in all. According to Picton a heart-body is found in the following groups : Spionidæ, Cirratulidæ, Terebellidæ, Ampharetidæ, Amphictenidæ, Chlorhæmidæ, Sternaspidæ, and Hermellidæ. He omits the Arenicolidæ, and states that in Magelona the organ is merely larval and transitory. As regards the Spionidæ, I am unable to find any confirmation as to its occurrence in this group. Possibly owing to a revision of the nomenclature the Cirratulidæ have been included twice in this list, under different headings.

M. Georges Bohn (9) shows how among Annelids adaptation to life in the sand is pushed further in some groups than in others, and divides the Polychætes, after excluding the Errantia, into three classes, according to the degree in which they have become adapted to a subterranean existence. In connection with this it is interesting to note that it is only in his third group, i.e. among those in which the burrowing habit is the rule, that the heart-body is present, and that all possess delicate respiratory filaments. Bounhiol, to whose paper reference has already been made, belittles the value of these processes for respiration, but the point is that they are not merely of value as gills pure and simple, but are often the seat of abundant cilia which ensure the circulation of water round the body itself. Thus in tubicolous forms serious damage to the processes is as dangerous as in Cirratulidæ or Arenicolidæ. In the Sabellidæ, which do not possess a heart-body, aeration of the body in the tube is obtained by the perpetual protrusion and retraction of the branchial crown, and here the branchiæ or tentacles are no longer soft and delicate, but are supported by an undoubted skeleton, whereas in the closely allied Hermellidæ, e.g. Sabellaria, where a heart-body is present, the " tentacles " and neuropodial processes are again of the delicate type.

GROUPS POSSESSING A HEART-BODY.

Family	*Habits.*	*Type of branchiæ.*
Cirratulidæ.	Permanent burrowers; with exception of one boring form.	Gills soft, delicate, and filamentous, capable of great elongation.
Terebellidæ.	Forms building tubes of sand or mud.	Gills, situated at anterior end, branched in most species, but all soft and delicate.
Ampharetidæ. } Amphictenidæ. }	Tubicolous.	Gills, situated at anterior end, delicate and filiform, capable of extension, e.g. *Pectinaria belgica.*
Arenicolidæ.	Permanent burrowers.	Gills branched and delicate.
Chlorhæmidæ.	Burrowers or inhabitants of tubes in mud.	Gills delicate and filiform.
Sternaspidæ.	Burrowers.	Gills delicate and thread-like.
Hermellidæ.	Tubicolous.	Filaments at anterior end are apparently not much used for respiration, but true branchial processes are present on the sides of the body. These are delicate, unbranched and covered with cilia.

The above table shows considerable similarity in the nature of the gills and habitat among the species of those families which possess a heart-body. The majority are burrowers, permanently subjected to pressure, and even in the tubicolous forms, seeing that they must often become sanded up (for instance, by wave shock when the tide is rising), the possession of a heart-body cannot but be advantageous in preventing regurgitation of the blood to the dorsal vessel, keeping the branchial processes turgid, and generally counteracting the effects of varying pressure. As a proof of this we note that the greatest development of the heart-body occurs in just those groups where burrowing habit and branchial development are carried to their greatest extent.

It is perhaps advisable to point out here that any mechanical function which is suggested on behalf of the heart-body is only regarded as secondary. There seems hardly any doubt that in the heart-body we are dealing with a structure the original function of which was almost, if not entirely, organic.

It may be urged that, according to this theory, one might reasonably expect to find the development of a heart-body in those other groups of M. Bohn's where the burrowing, free-swimming, and crawling habits are combined, e.g. in the Aphroditidæ, Phyllodocidæ, Nephthydidæ, Glyceridæ, Eunicidæ, Ariciidæ. In these groups, however, apart from the fact that, owing to their semi-active habits, the danger of asphyxiation is considerably reduced, the branchial processes themselves are in most cases effectively protected by the great development of the parapodia and chætæ. This is excellently exemplified by the condition in Nephthys, where the sickle-shaped gill is situated between the strongly developed lobes of the parapodia and their lengthy chætæ.

As we pass to the consideration of forms with more and more predominantly burrowing habit we note the concurrent reduction in size of the chætæ, for, useful as they undoubtedly are in swimming and crawling, they can only be a hindrance to progress in and through sand. The bristles acquire more and more the character of short hooks, enabling the animal to grasp the side of its burrow, and, if the gills are to be retained, a new method of protection must be adopted.

Method of Feeding.—I will now examine the specialised method of feeding in Cirratulus in more detail. Unlike its congener in the same habitat, Arenicola, Cirratulus does not live by passing sand through the gut; selection of the nutritive organic particles is made outside the body. The excreta are green in colour, and the worm's diet would seem to consist of algal spores, fragments of decaying algæ, diatoms, and general organic debris. In preparing the worm for sectionising no special precautions were taken to ensure the emptying of the gut, and the razor did not suffer.

The best proof of the microscopic nature of the animal's food is the ciliated condition of the gut. It remains to be seen by what means the animal is able to exercise selection.

On the ventral side of the peristomium a deep groove leads back to the mouth and is continuous with the dorsal surface of the gut. On the walls of the pharynx immediately behind the mouth opening are situated a pair of flaps. These flaps are dorso-lateral in position and project each with its free edge standing out ventrally towards the median line (see Figs. 1–7).

Fig. 1.—Transverse section through the anterior portion of the peristomium, showing the ventral groove.

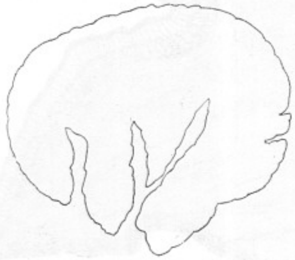


Fig. 2.—Transverse section behind Fig. 1, showing the development of the sensory flaps.

Fig. 3.—Section through the peristomium, somewhat anterior to the line AB in Fig. 7.

The two free edges are closely apposed and thus practically separate a groove above them from the remainder of the vestibule beneath. The epithelium of this groove and of the surfaces of the flaps which face inwards, including the free edges, is ciliated and rich in sensory elements, and is most markedly distinguishable from the general epidermis and from the lining of the vestibule, the floor of which projects forwards and seems glandular. The ciliated epithelium of the gut has already been noticed. The animal would thus seem to feed by a kind of suction; the sensitive edges of the flaps being closely apposed would effectively prohibit the entrance of any but the smallest food particles, and these latter would be wafted backwards by the cilia of the gut epithelium.

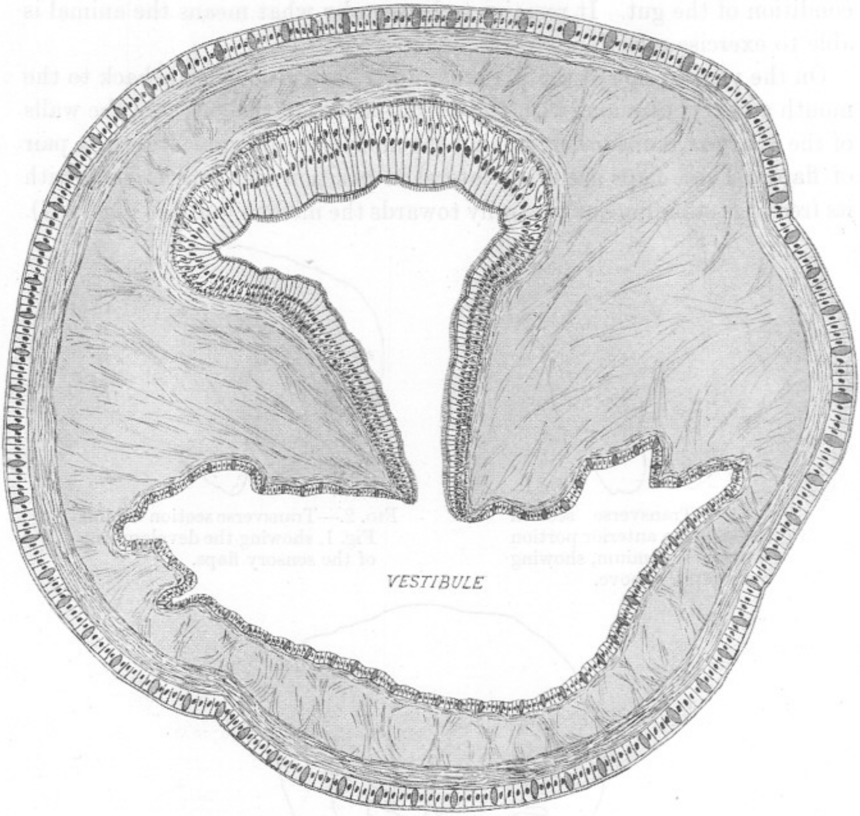
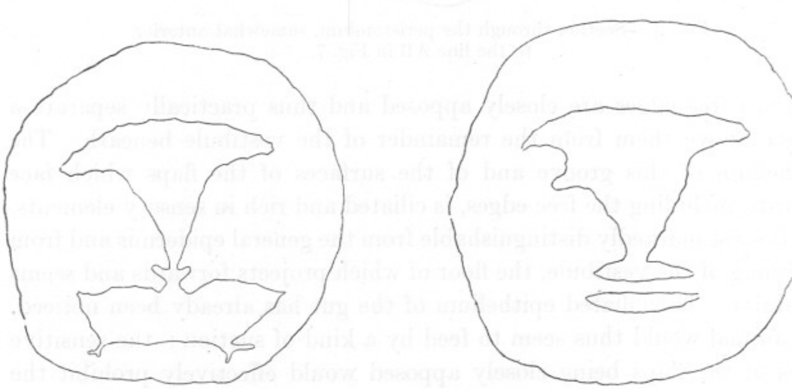


FIG. 4.—Transverse section through A–B in Fig. 7, showing the sensory lips and the ciliated epithelium of the gut.



FIGS. 5 and 6.—Sections showing the gradual disappearance of the vestibules and the fusion of the sensory flaps with the sides of the pharynx.

In view of such a method of feeding, the idea of a food-catching function on the part of the filaments must be rejected. Moreover, as the mouth of the worm in its burrow is situated some distance beneath the surface and the filaments are waving in the water above, how is any such function practicable ?

I am convinced that it is only under direst necessity that Cirratulus quits its burrow, and then it is certainly not to swim about actively, as M. Bounhiol suggests, but merely to crawl sluggishly on the surface of the mud. If by an accession of clean water the symptoms of asphyxia are removed, the worm will immediately recommence burrowing.

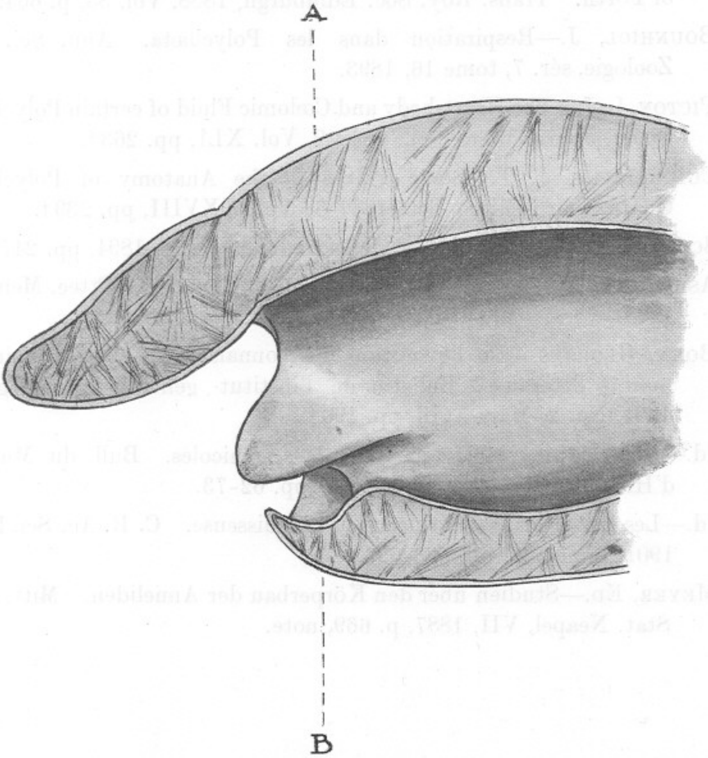


FIG. 7.—Diagrammatic median longitudinal section through the anterior end of Cirratulus.

Nor are the filaments used to collect sand particles. Sand particles adhere to the mucus exuded by the body of the worm, and by so doing probably prevent the walls of the burrow from caving in. They thus allow the animal greater freedom of movement, but there is certainly nothing that can be dignified by the name of a tube.

In conclusion, I wish to thank Mr. F. S. Wright for his able execution of the drawings for half-tone blocks for this paper.

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