THE LUGWORM (ARENICOLA) – A STUDY IN ADAPTATION
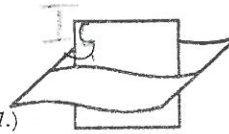
by

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It is indeed a pleasure to be present at the Wadden Sea Symposium, and to join in this tribute to Dr. Verwey and the fine laboratory which he has directed for so many years. The subject suggested to me by your Committee—"different aspects (morphological, physiological, behavioural, etc.) of the adaptation of one particular species to its milieu"—is one in which I have long been interested, and my purpose today is, not to announce new discoveries, but to re-examine a number of results, some pretty old and some rather younger—to see whether they can be persuaded to fit together in a biologically meaningful way. The "particular species" is a well-known inhabitant of the Wadden Sea, and some of the most important work on it has been done in this region. I refer to the European lugworm, *Arenicola marina* (L).

"Adaptation to milieu". The line of approach that the phrase immediately suggests is to start by describing the environment, and then to go on to a discussion of the ways in which the animal has improved itself, in the course of evolution, for life in such surroundings. But at once a difficulty appears. The lugworm lives in a burrow. That is to say, it makes its own environment to some extent, and what it has adapted itself to, in the course of evolution, is a particular way of life.

We have here a complex situation. The animals behaviour is adapted to its environment. On the other hand, its immediate environment is formed by its behaviour. So our discussion of the lugworm's adaptations must be based on knowledge, not only of *where* but also of *how* it lives, and I shall begin by summarising what is at present known about its essential activities.

THE LUGWORM'S WAY OF LIFE

The lugworm has a number of alternative modes of behaviour. For much of the time it lives quietly in its burrow, eating the sand and ejec-ting the well-known sand castings. But there are other ways too in which it can behave. For example, it can migrate from place to place on the beach, it has special behaviour patterns associated with breeding, and so on. We shall have to remember, in discussing its anatomical and physiological adaptations, that not all of its life is spent in a burrow.

However, the most thoroughly analysed of its behaviour patterns, and the one to which it devotes the largest share of its time, is so spent. The description of this pattern now follows, and, to distinguish it from the various possible alternative patterns, I shall call it the Normal Cyclical Pattern, or N.C.P.

The Normal Cyclical Pattern appears in its most typical form when the surface of the sand is covered by water. This may occur on the beach at high tide, or under a shallow sheet of water at low tide, or in a tank in the laboratory. The pattern is characterised by the ejection of the faecal cylinders, which appear one by one, at regular intervals of time, and also by the corresponding subsidence of the sand surface over the other end of the burrow. It may continue, regularly and uninterruptedly, for many hours, and the faecal cylinders may steadily build up into a very large pile.

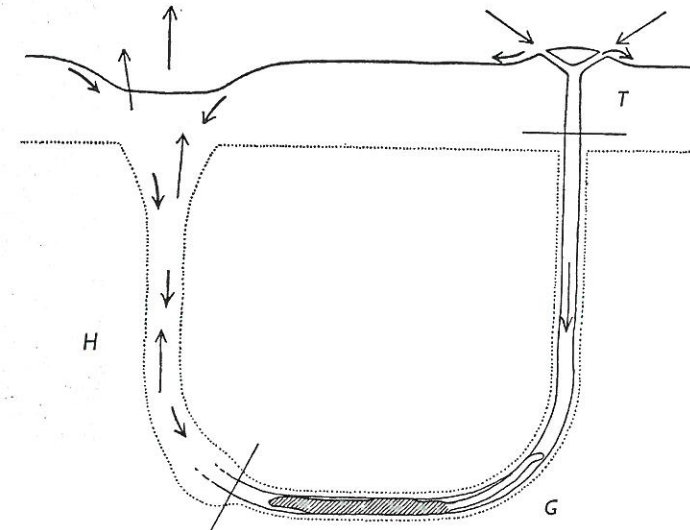The essential structure of the burrow, the special environment in which

Fig. 1. Generalised diagram of a lugworm burrow. The cross lines are drawn at the boundaries between head shaft (H), gallery (G) and tail shaft (T). The dotted line is the boundary between yellow and black sand. Long, thin arrows show the movement of water, short, thick ones that of sand.

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the N.C.P. is performed, was first clearly described by THAMDRUP (1935), although the picture he drew has since been developed and extended (LINKE. 1939; WELLS, 1945). The burrow consists of two main parts, called the gallery and the head shaft (Fig. 1).

The gallery descends from below the pile of faeces. Its walls are impregnated, to a thickness of several millimetres, with the worm's secretions, which make them firm. Sometimes, on beaches which are being gently washed away, the galleries stand up from the general surface like miniature drain pipes, because of the secretions that bind the sand together (LINKE, 1939). The worm moves to-and-fro in the gallery, keeping its head towards the head shaft. Above, the gallery narrows to become the tail shaft, through which the tail is thrust at the moment of defaecation.

The head shaft varies considerably in form. Typically, it is a descending column of sand, resembling the surface sand in its yellow colour. At the upper end is a funnel, or a shallow saucer, or some other sign of subsidence. At the lower end, where the worm feeds, there is usually an accumulation of rejected material (shell fragments, small stones, etc.). On beaches densely populated by lugworms, these accumulations may unite into a definite layer of coarse material from which the finer particles have been removed by feeding; the layer lies at the level of the deepest part of the burrows (VAN STRAATEN, 1952; 1956). The substance of the head shaft is rather more fluid than the general sand, and it is not sealed off by any secretion-impregnated boundary layer. Its separation from the surrounding material must be minimal on densely populated beaches, where a layer of coarse material has been built up, for water can circulate quite freely through such a layer, under tidal and other influences.

The worm pumps water through its burrow, in a tail-to-head direction, by means of piston-like waves that run along its dorsal surface (JUST, 1924; VAN DAM, 1937, 1938). Most of the water so pumped returns to the surface along the head shaft. The irrigation stream brings oxygen, sweeps away soluble excretory products, and also acts as an important source of food, for it brings suspended particles that get trapped in mucus at the lower end of the head shaft and are duly swallowed with the material of the shaft (KRÜGER, 1958a, 1962). Because of the oxygenated water stream, the walls of the gallery are yellow, often in contrast to the surrounding grey or black.

The N.C.P. can be investigaged by taking advantage of two fortunate facts, Firstly, the irrigation stream fluctuates according to the worm's other activities, and there are also big displacements of water when it creeps forwards or backwards. These water movements can easily be traced on a kymograph in the laboratory, and so the worm's activities
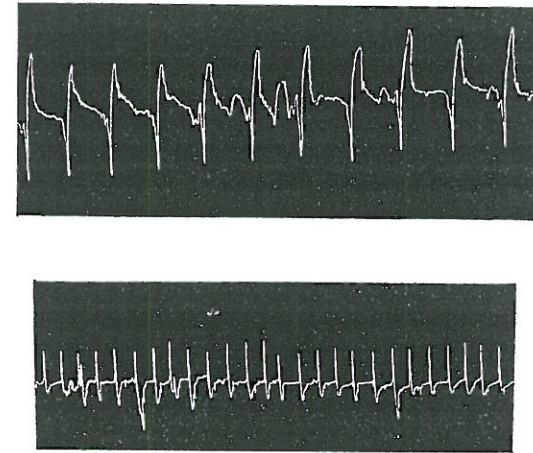
Fig. 2. The N.C.P., illustrated by two water-movement records written by worms in sand in the laboratory. Both records are 7 hours long, and should be read from left to right. In the upper record, a downward movement of the writing point means a tailward displacement of water; defaecations occur at the sharp needles which terminate the tailward excursions. In the lower record the pattern is reversed because the recording device was connected to the other end of the burrow; the worm was much smaller so defaecations occur more frequently.

can be recorded continuously for many days (WELLS, 1949b). A special method was recently devised by KRÜGER (1964), for taking records from burrows in the field. Secondly, under appropriate conditions the worms will perform the N.C.P. in glass tubes in the laboratory; the various component acts of the N.C.P. can then be watched, and the records of water movements can be interpreted.

A characteristic feature of the N.C.P. is the repetition, at regular intervals of time, of the following sequence of events: the worm first creeps backwards to the sand surface, then ejects a sand cylinder, then slowly returns to the bottom of the burrow, meanwhile pumping water with exceptional vigour. These sequences appear as diphasic excursions on the water-movement records (Fig. 2). The intervals between them are generally about 40 minutes in large worms, but less in small ones (e.g. 15 minutes in worms weighing 2–3 gm, WELLS, 1953).

A curious point about the excursions is the following. In the first stage, of backwards creeping, waves of swelling run in a tail-to-head direction along the worm's body. These waves act as fixed points, so that the worm moves backwards. One might therefore suppose that the return to the bottom of the tube is due to waves travelling in the opposite direction,

i.e. from head to tail. But this is not so. The waves still run headwards. It has been observed several times, that the worm can move slowly forwards along a tube during vigorous headward pumping ("synkinetic locomotion"; (JUST, 1924; WELLS, 1949a). The excursion consists essentially of a burst of vigorous headward peristalsis, divided into two distinct parts by a pause, and the sudden ejection of a faecal cylinder.

It would be easy to make another wrong guess too, and to suppose that the excursions depend on chain reflexes. A full rectum might be thought to stimulate the backward trip, and the relief following defaecation to stimulate the return. But such a view is certainly incorrect. Sometimes a worm will perform the typical sequence over and over again, at very regular intervals of time, when kept in a glass tube without food and therefore without faeces to discharge. Close inspection of the tracings suggests that it even makes an effort at ejection at the appropriate moment. By this experiment and others, it has been shown that the excursions are released by a spontaneously active pacemaker built into the worm, and probably located in the ventral nerve cord (WELLS, 1949a).

In the intervals between the excursions, the worm drives water through the burrow at a fluctuating rate. The fluctuations are caused by the impact of other activities of the worm, going on at the same time. For example, it feeds in short bursts, each of a few minutes' duration, and each burst is accompanied by a partial inhibition of pumping. The feeding bursts are released by a second spontaneously active pacemaker, located in the wall of the oesophagus (WELLS, 1937; 1949b, 1957; WELLS and ALBRECHT, 1951). There is also the rhythmic emptying of the nephridial bladders, which happens every minute or two, and commonly just after the passage of one of the pumping waves (STRUNK, 1930).

The N.C.P. is in fact an extremely complicated fugue, in which many recurrent rhythms are combined to build an integrated pattern.

And now, for some of the alternative patterns or fugues performed by the worm. These are not yet so well analysed as the typical N.C.P. Some of them are evidently modified versions of the typical N.C.P., while others are quite distinct.

Two of the modifications are especially interesting. The first is a method of aerial respiration. It can sometimes be seen if a worm is placed in a glass U-tube with only a little water at the bottom, so that water circulation is impossible. Every now and again, the worm makes a backward excursion to the water surface and draws air bubbles over its gills by means of waves running headwards along its body. After a pause, it returns to the bottom of the tube again (WELLS, 1945, 1949a). The excursions occur at intervals similar to those that separate the excursions of the typical N.C.P., to which they are clearly related.

This behaviour probably occurs in the field, at low tide, if a low

groundwater level prevents circulation by pumping. *Arenicola* is known to prefer situations where the beach retains a surface layer of water, or at least stays soft and moist, at low tide (THAMDRUP, 1935; WOHLENBERG, 1937). One has to admire the adaptability of its N.C.P., which allows the worm to carry on with its business as usual, in a variety of low tide conditions.

The second modification is seen in the laboratory when conditions get really bad—for example, when the worm is imprisoned in a closed circuit of water which cannot be aerated or renewed. The oxygen content therefore falls, and metabolic end-products accumulate. As the environment deteriorates, the worm becomes almost completely passive. To a human observer, it looks drowsy. But every now and again it makes a "testing" excursion, moving slightly backwards and tentatively pumping a little water. As in the first modification, the intervals are about the same as those of the typical N.C.P., and the worm seems to bo obeying the same pacemaker. If the experimenter admits new water to the system, the worm discovers the fact at its next testing excursion, and immediately becomes vigorously active (WELLS, 1949a).

One can imagine circumstances arising in the field from time to time, which would cause the worm to respond in this way. Once again, one cannot help admiring the versatility of the N.C.P.

Some of the recorded modifications of the typical N.C.P. may be artefacts due to laboratory conditions. Worms kept in glass tubes without food have a low level of activity, and generally suspend their pumping between the excursions of the N.C.P. ("Ventilationspausen": VAN DAM, 1937, 1938). Such pauses never occur when the typical N.C.P. is carried out in sand, either in the laboratory or in the field (KRÜGER, 1962, 1964). Occasionally, however, patterns which seem to be simplified versions of the N.C.P., without feeding or defaecation, have been recorded from worms in sand in the laboratory; these, too, may be artefacts (WELLS, 1949b).

The worms can also produce behaviour sequences with no detectable relation to the N.C.P., but our knowledge of these is very meagre. In a study of the behaviour patterns of a series of worms kept in sand in the laboratory, I found that their time was divided as follows: typical N.C.P., 45%; modified versions of the N.C.P., 5%; unexplained activity, 35%; no apparent activity, 15% (WELLS, 1949b).

The periods of no activity should not be confused with the "Ventilationspausen" mentioned above. They lasted for many hours on end—even for 24 hours. During this time no water movements were recorded, but afterwards the worms became active again. What, if anything, they were doing is a mystery. Their prolonged inactivity might be yet another laboratory artefact.

The periods of unexplained activity in my experiments could also continue for many hours. The lever showed excursions, often of great amplitude, but the patterns bore no evident relation to the N.C.P. The worms, of course, were invisible in the sand, so their behaviour could not be watched. Similarly, the records taken in the field by KRÜGER (1964) show long periods of activity that cannot yet be interpreted in detail. He described how they often reverse the normal direction of pumping for prologed periods when the tide rises over the beach, and suggested that this might be a period of reconstruction or repair of the head shaft.

When watching worms in glass tubes, one sometimes sees activities that play no part in the typical N.C.P., and may perhaps be components of the unexplained patterns traced by worms in sand. There is, for example, the "drag cycle", an elaborate sequence of acts in which the worm looks as if it were trying to drag surface sand, or other materials, into a head shaft, or perhaps to stir up the substance of the shaft itself (WELLS, 1945).

Finally, there are various behaviour sequences that are carried out in the absence of an established burrow. Lugworms have often been found swimming, and are known to migrate from place to place on the beach (THAMDRUP, 1935; WOHLENBERG, 1937; SMIDT, 1951; WERNER, 1954, 1956; NEWELL, 1948). And of course there is the sequence by which a worm, dug out and replaced on the surface, will make its way back into the sand (TRUEMAN, 1966). No doubt, under natural conditions, this follows swimming and is itself followed by the building of a burrow of the characteristic form. However, the worm becomes extremely sedentary if it happens to find a situation to its liking. LINKE (1939) has described the continuous occupation of marked burrows for eight months and it should not be forgotten that the species extends for some distance below the tidal zone, to places where conditions are more uniform, becoming in fact exclusively sublittoral in the icy Northern part of its range.

There seems little room for doubt that the N.C.P. is the worm's regular routine, a pattern of contentment to which, other things being equal, it tends always to return.

THE INDIAN HOG – A WARNING

Before going on to some examples of how the lugworm's organisation is adapted to suit its way of life, I want to tell you a story about the so-called Indian hog. It contains a salutory warning.

In 1802, William Paley, a philosophical English divine, published

his "Natural Theology", in which he described example after example of what looks like design in nature. Design, he argued, is evidence of the existence of a Designer. His enthusiasm led him to include in his collection several examples that nowadays look rather ridiculous, and among them the following, which I shall quote in his own words. The story was current in the natural history books of his time, so Paley should not be blamed too much for putting it in.

"It is always an agreeable discovery, when, having remarked in an animal an extraordinary structure, we come at length to find out an unexpected use for it. The following narrative furnishes an instance of this kind. The babyrouessa, or Indian hog, a species of wild boar, found in the East Indies, has two *bent* teeth, more than half a yard long, growing upwards, and (which is the singularity) from the upper jaw. These instruments are not wanted for offence; that service being provided for by two tusks issuing from the upper jaw, and resembling those of the common boar; nor does the animal use them for defence. They might seem therefore to be both a superfluity and an encumbrance. But observe the event: the animal sleeps standing; and, in order to support its head, hooks its upper tusks upon the branches of trees."

Nowadays the hunt for design is still on, though, as biologists, we substitute "natural selection" for the Designer. In other words, the functional aspect of biological organisation is still a fascinating branch of study. But there is danger in the pleasure which the discovery of an unexpected function can yield, for the pursuit of that pleasure may lead us to excess—to the uncritical acceptance of ingenious adaptive explanations, in disregard of the warning so plainly given by the tale of the Indian hog.

MODIFICATIONS OF THE METAMERIC PLAN

I turn now to some examples of how the gross anatomy of the lugworm's body appears to be adapted to its way of life.

The worm is built on the metameric pattern. It consists of a series of segments, each of them having the same basic design. The remote ancestors of *Arenicola* probably resembled in general appearance the errant polychaeta of today, such as *Nereis*, and were composed of segments that did not differ very greatly from each other—each having a pair of parapodia, a pair of nephridia, and so on. But in *Arenicola* the segments have undergone divergent specialisation, in such a way as to divide the body

into distinct regions (Fig. 3). We may ask how the resulting organisational patten is adapted to the conditions in which the worm lives.

Most conspicuous of the lugworm's differentiated regions is the tail, and this can be explained as a device for communicating with the surface with minimal risk. The worm is comparatively secure as long as it stays deep in the sand. But its backward excursions to the surface, for defaecation, expose it to a host of predators—sea birds at low tide, crabs and fishes at high—Now the distinctive features of the tail are these.

(i) It is highly sensitive, and shortens rapidly by means of a giant-fibre reaction if stimulated at the tip. This response reduces the probability of loss, on the approach of a predator.

(ii) It consists of little more than a sand-filled rectum ensheathed by a muscular body wall. The vital organs—hearts, gills, stomach, nephridia, gonads—are placed further forwards in the body. So the severity of such losses as predators may inflict will not be great, as long as they are limited to the tail.

(iii) If the end segments are seized and held, the tip of the tail can be automised. The break happens at an intersegmental boundary, in such a way that there is very little bleeding (LINKE, 1939).

(iv) The tail has a special method of renewal by backward growth. The body of a lugworm is laid down in the first place by a growth-zone at the hinder end. This growth-zone forms the 19 segments of the trunk, from before backwards. Having reached the hinder end of the trunk, it produces an enormous number of very short tail segments. These lengthen as the worm grows up, the hinder ones lengthening first. The segments at the front of the tail are a reserve stock, producing more tail as they lengthen in their turn, in later life. One might expect that renewal of the tail occurs only in response to accidental losses, but in fact it goes on all the time, and segments are shed at the tip by autotomy if they have not been accidentally lost. The European lugworm is believed to produce, during its lifetime, an amount of tail equal to at least five times the total length of the adult worm (WELLS, 1950).

The lugworm's tail can be likened to the protection money exterted by gangsters. It is something the animal produces all the time, to placate the predators of the world above the sand. As for the other parties to this arrangement, the predators have several times been described as feeding on lugworm tails. For example, STACH (1944) wrote the following, about the Australian *Arenicola loveni sudaustraliense* at low tide: "The oyster catcher, *Haematopus fuliginosus*, was often observed to peck off the tails of lugworms extruding their castings". And BLEGVAD (1930) wrote, of the diet of young plaice (1–2 years old) in the Kattegat; that worms predominate in the food, especially *Nephthys*; "as No. 2 in frequency ... come hind parts of *Arenicola marina*; it seems to be a fact that the plaice
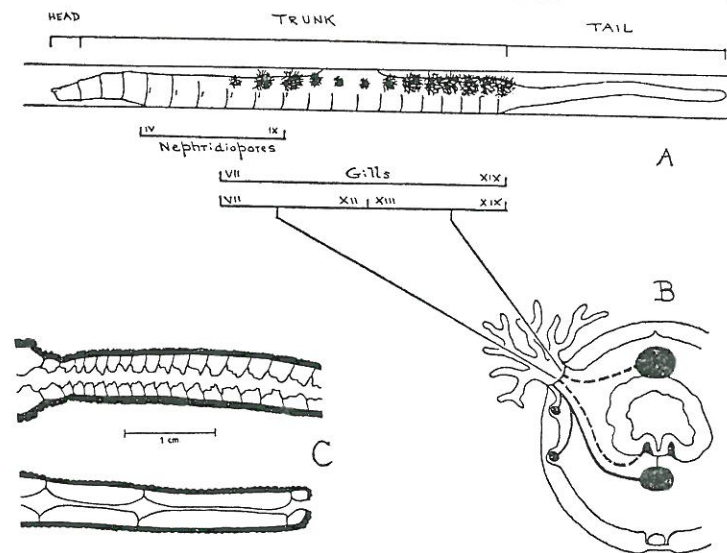
Fig. 3. A: a worm driving water in a headward direction through its tube. A piston wave is passing two of its gills, which contract as the wave goes by. Some of the more interesting regional differentiations are indicated.
B: diagram of the branchial circulation. The branchial afferent (black) runs from the ventral vessel to the gill, receiving contributions from the body wall on the way. The efferent (broken line) has two alternative courses. It runs to the dorsal vessel in the hinder branchiate segments, but to the subintestinal in the more anterior ones.
C: horizontal sections through the base and tip of the tail of a lugworm of total length 140 mm. Notice how the tail is renewed by the lengthening of "reserve segments" at its base.

bite off the *Arenicola's* hind part when it is thrust out of the sand in order to deliver the faeces".

The picture should be extended to include other dangers, besides predators. The falling tide often leaves shallow pools or sheets of water over the burrows of *Arenicola* and these may become hot enough, in bright summer sunshine, to injure the worms, while the underlying sand remains quite cool (LINKE, 1939). A heavy rainfall, or a hard frost, might make the surface dangerous. In any of these situations, it is clearly best for the worm that the expendable tail should approach the surface first.

Turning now from the tail to the 19 segments of the trunk, we find here considerable differences between segment and segment, and these also can be interpreted as adaptations to the worm's way of life. The different development of the parapodia at the two ends of the trunk affords a very clear example.

The first few segments are especially concerned with burrowing and certain related movements, while the rest are mainly responsible for locomotion and water pumping, and the anatomy of the parapodia shows corresponding variations. There is no need for me to give details on this point; the movements, and the responsible structures, have been described very fully in the literature (JUST, 1924; WELLS, 1950, 1944, 1961).

I want to spend a little time on two other examples of intersegmental differentiation. Both have been explained as adaptations to the water current pumped by the worm, which flows, nearly always, in a tail-to-head direction. As I believe that these explanations, though tempting, are not quite secure, I want to discuss them as critically as the available information allows.

The first is the distribution along the body of the gills and nephridia. The gills are restricted to the hinder thirteen segments, and the first pair or two are noticeably smaller than the rest. Nephridia occur only in a few segments near the anterior end (Nos. iv–ix, in *A. marina*). The obvious explanation is that this distribution minimises the chances of resorption, through the gills, of the worm's excretory products.

Can we produce any physiological evidence in support of this idea? The urine of the lugworm has never been analysed, as far as I know. On comparative grounds, we would expect the chief nitrogen compound to be ammonia, a notoriously toxic substance. According to STRUNK, the body fluid contains small amounts of urea, and many of the organs contain urease. Injection of only a small amount of additional urea—enough to raise the existing concentration by about 10%—was lethal, apparently because of its conversion to ammonia by the urease (STRUNK, 1932, 1935). These results support the idea that the resorption of ammonia through the gills would be a bad thing. Once, while studying aerial respiration, I noted that an *Arenicola* lived for 5 days in only 15 ml of water, without ill effects (WELLS, 1949a). This could be understood if the nitrogen is excreted in a volatile form, which can escape into the air. On the whole the physiological data, though regrettably meagre, are at least not in opposition to the explanation.

The second differentiation concerns the course of the branchial efferent vessels. All of the gills receive their blood in the same way, partly from the ventral vessel and partly from the body wall. But they send it away in different directions. The hinder seven pairs send their blood to the dorsal vessel, while the front six pairs send it to a component of the gastric plexus, on the ventral side of the stomach (fig. 3).

Why this difference should exist is rather a puzzle and the following explanation has been suggested (WELLS, 1963). The water stream flows, first over the hinder gills and then over the front ones, so the water in

contact with the front gills has already given up some of its oxygen and received carbon dioxide. We may infer that the blood returning from the hinder gills is the best, and it is this blood which is sent to the dorsal vessel, and so directly forwards to the head.

The following comments may help us to evaluate this explanation.

(i) It seems that under high-tide conditions, the blood can take up quite as much oxygen as the tissues require, even from the water in contact with the foremost pair of gills. According to VAN DAM (1938), the lugworm can withdraw up to 50% of the dissolved oxygen in the water pumped past its gills. According to the careful respiration measurements of KRÜGER (1958b), its oxygen consumption is independent of concentration down to a critical value of about 0.7 ml O_2/l., which is very much lower than the amount found by VAN DAM in the water which has passed over the gills.

(ii) At low tide, the oxygen content of the interstitial water, and also of the water in the burrows of *Arenicola*, may fall below the critical value of KRÜGER; this was shown by analyses made on the Yorkshire coast by JONES (1954) and in the Wadden Sea by ELIASSEN (1956). However, the explanation as set out above depends on the existence of a headward stream of water, and there will be no shortage of oxygen in the water as long as such pumping is possible.

(iii) There may be important differences between the environments of the posterior and anterior gills if, under low-tide conditions, the worm resorts to aerial respiration, for very often the air bubbles reach only the gills at the hinder end of the series. But this does not really help us if, as is commonly supposed, the haemoglobin is being used at that time in storage rather than in transport. If the blood is oxygenated as a whole from the air bubbles, to provide a store that can be used in the subsequent period of immersion, the details of the circulation paths during the stocking-up period would seem to be unimportant.

(iv) It may be that the distinction between "good" and "bad" blood should be based more on carbon dioxide than on oxygen tension. Under high tide conditions, the CO_2 tension will be only slightly raised, and the pH only slightly depressed, in the water flowing past the gills, because sea water has a strong bicarbonate buffering system. We have at present no experimental evidence on the sensitivity of *Arenicola* tissues to small changes in these variables. It would be interesting to take up again the question of the "drowsiness" of *Arenicola* imprisoned in a closed water circuit, and find out whether the immediate cause is oxygen lack, or CO_2 excess, or perhaps some other metabolite. The behavioural change occurs quickly (WELLS, 1949a), so there must be something to which the worm is pretty sensitive. If that "something" should turn

out to be a soluble metabolite escaping through the gills, we should have positive support for the explanation. But at present, it must be admitted, we have none.

If I spent rather too much time in discussing the last example, the reason is that I published the explanation myself, a few years ago, when, in a moment of enthusiasm, I forgot about the Indian hog.

SPECIALISED BEHAVIOUR SEQUENCES

It will be clear, after what has already been said, that the Normal Cyclical Pattern is beautifully adapted to the worm's way of life, and this may be an appropriate moment to emphasize the point, for we have just been discussing morphology and the N.C.P. is, after all, an organised form—a pattern of acts arranged in time. But whether or not the moment is appropriate, the occasion most certainly is, for you, Dr. Verwey, have published illuminating discussions of the "more or less complcated innate series of actions, in which the structures and behaviour are equally specialised", as shown by marine animals of many kinds (VER-WEY, 1949). The lugworm provides one more example.

HAEMOGLOBIN

As an example of physiological adaptation, I shall take the properties of the haemoglobin in the lugworm's blood. These have often been discussed in the past, but the picture changes all the time, as we discover more about the haemoglobin, and also more about the worm's habits and needs.

There was an unfortunate tendency, in some of the earlier discussions of this topic, for the investigator to adopt what I can only call a patronising attitude towards his animals. The idea was widely held at one time, that because the worm has red blood, and hearts, and gills, it must be trying to do, in its lowly and inefficient way, the same things with its haemoglobin that we do, so much better, with ours.

We were taught, when I was a student, how the haemoglobin of worms is diffused through the blood plasma while ours is located in erythrocytes, and the withdrawal of our pigment into a favourable environment, sheltered from the complicated and fluctuating chemistry of the plasma, was represented to us as a great evolutionary advance. But nowadays it seems probable that the condition found in worms is the more sophisticated of the two. The ancestral plasma was sea water; the ancestral

haemoglobins were descended from a family of haem compounds inside the cells; the liberation of haemoglobin into the plasma was therefore a forward step. Its main advantage, as suggested by REDFIELD (1933), may be that the worm's haemoglobin can add to its other functions the osmotic one performed by our own serum proteins, of controlling the leakage of blood through the capillary walls.

In the matter of its reversible combination with oxygen, there are two great differences between lugworm haemoglobin and our own. The first is its much higher affinity for oxygen. Lugworm haemoglobin is half saturated at about 2 mm O_2, ours at about 27 mm. The second difference concerns the Bohr effect, the flattening action of CO_2 on the oxygen dissociation curve which makes so important a contribution to the efficiency of transport by human blood. This effect is very slight in *Arenicola marina* and absent altogether in several North American species (WOLVEKAMP and VREEDE, 1941; MANWELL, 1964a).

In view of these facts, it may seriously be doubted whether the haemoglobin of *Arenicola* plays any part at all in oxygen transport. The oxygen tensions in the tissues are unlikely to fall low enough to pull oxygen away from the haemoglobin while the worm is pumping well-oxygenated water through its burrow. Under these conditions, transport must be accomplished by physical solution in the blood. Perhaps the haemoglobin could play a part in transport when the external oxygen tension is low. In this connection, it may be recalled that ELIASSEN (1956) found a variation in the oxygen capacity of the blood of individual worms from 1.4 to 8.9 vols per cent., and if we correct these figures for oxygen in physical solution, they indicate that the haemoglobin concentration is nearly ten times as great in some worms as in others. This hardly looks like a transport system closely adjusted to the animal's needs.

Several writers have suggested that the haemoglobin can act as an oxygen store (VAN DAM, 1938; BARCROFT and BARCROFT, 1924) and such an action seems to be very likely in some circumstances; in aerial respiration, for example, the haemoglobin could be oxygenated during the exposure to air, and the oxygen used during the subsequent period of submergence. Attempts have been made to calculate the length of time for which the store would last, but this probably varies greatly with the known variation in haemoglobin content of the blood.

New light has been thrown on the whole problem in recent years by the suggestion that *Arenicola* haemoglobin includes among its functions the protection of the worm against two different poisons.

The first of these poisons is oxygen itself. According to FOX and TAYLOR (1955), many invertebrates, especially those living in marine or freshwater muds, are slowly poisoned by oxygen excess, even at atmospheric tension. To keep such animals healthy in aquaria, it is better to bubble

the water with a mixture of one part of air to four of nitrogen than with air alone. FOX and TAYLOR found that *Arenicola marina* lived equally well, whether bubbled with air or with the low-oxygen mixture; the worms were injured by bubbling with pure oxygen[1]. It would be very interesting to make oxygen-tolerance experiments, not on whole worms but on isolated tissues, for in the whole worm the tissue tensions are lower, to an unknown extent, than those outside. If we may suppose that the tissues of *Arenicola* are adversely affected by oxygen excess at tensions below the atmospheric tension, the peculiarities of the oxygen dissociation curve become intelligible. Whether the haemoglobin acts as a transport vehicle or as a store, the high oxygen affinity and the partial or complete suppression of the Bohr effect ensure that its oxygen will only be delivered when supplies are really needed, and the local tensions therefore really low. In a word, they are precautions against injury by over-generous supplies (MANWELL, 1959).

The second poison, to which attention has been drawn by PATEL and SPENCER (1963a, b), is hydrogen sulphide. The investigators started from the observation that the worms are often found in habitats where they must sometimes be exposed to hydrogen sulphide from the surrounding mud. Hydrogen sulphide is of course well known as highly toxic to mammals; it inhibits several enzymes and also interferes with oxygen transport by forming the compound sulphaemoglobin. On the other hand, haem compounds are known to catalyse the oxidation of sulphide, and it seemed possible to PATEL and SPENCER that *Arenicola* might protect itself by using a haem compound for this purpose.

They found at once a property of the haemoglobin which, in their words, "must afford the animal considerable protection against the toxic effects of sulphide"[2].

The haem part of the molecule appears to be the same in worm and mammal. Prepared as haemin from the blood of either, it vigorously catalyses the oxidation of sulphide. When combined with protein to form haemoglobin, its catalytic action is greatly lowered, and this, too,

[1] MANWELL (1964b) wrote: "*Arenicola* of various species will live only a week or two at $P_{0_2} = 150$ mm Hg, though there is some individual variation". This is a curious result to find with an animal which so persistently irrigates its burrow. It would be interesting to have further details, especially about the conditions under which his animals were kept.
[2] SVESHNIKOV (1963) compared population densities in muds of different sulphide content and concluded that *Arenicola marina* is substantially more resistant than *Mya arenaria* or *Macoma baltica* to sulphide in the interstitial water. HECHT (1932) found experimentally that the resistance of *Arenicola marina* to sulphide was high, but exceeded by that of certain undetermined Nereids. As far as I know, the sulphide relations of polychaete haemoglobins other than that of *Arenicola* have not yet been investigated.

is true in worm and mammal. The significant difference between the two is this: that *Arenicola* haemoglobin is easily converted into a so-called "brown pigment" in which the link between protein and haem is broken or at least modified; this conversion abolishes the inhibitory effect of the protein and the catalytic activity of the "brown pigment" is as great as that of free haemin.

The "brown pigment" exists, in variable amounts, in the blood, side by side with haemoglobin. Moreover, it is produced instead of sulphaemoglobin when hydrogen sulphide acts on lugworm haemoglobin, so the poison, by liberating the haemin, accelerates its own destruction.

This protective mechanism may help to explain a curious anatomical feature of the worm, that has been noticed by every student who has dissected a specimen. This is the enormous amount of brown tissue, commonly described as excretory, but recently shown to be concerned with haemoglobin formation.

The ventral vessel has a "hairy" appearance, because it carries great numbers of blind side branches covered with darkly pigmented epithelium. As the worm grows, these side branches get more and more numerous and in time they begin to appear on other vessels too. In large, dark-coloured animals, the system of blind pigmented vessels is enormously developed.

It was recently shown that the cells manufacture haemoglobin, apparently in periodic outbursts, for the process occurs in an orderly sequence of stages, and all of the cells, in any one animal, are in the same stage (ROCHE *et al*, 1961). Perhaps he great variation in haemoglobin concentration found by ELIASSEN (1956) is due to this periodicity of production.

Further—as if this were not enough blood-forming tissue—the cavity of the heart is invaded by a so-called "heart body". This, too, increases in relative size as the worm gets older, and appears to be another centre of haemoglobin formation (KENNEDY and DALES, 1958; MANGUM and DALES, 1965).

Why this tremendous amount of haematopietic tissue? If a lugworm's haemoglobin had the same function as ours, i.e. to combine reversibly with oxygen and help in buffering against carbon dioxide, the existence of so extensive a blood-forming apparatus would be hard to understand, for these are processes in which haemoglobin is not used up. If, on the other hand, the function (or *a* function) of the pigment is to deal with invasions of sulphide, a process in which it is irreversibly converted into something else, the presence of the vast production apparatus is less surprising.

But I am wandering off again towards the quicksand of unsupported speculation.

The new discoveries raise all sorts of interesting problems that will have to be attacked in future research. For the present, our estimates of their functional significance must necessarily be tentative. One thing they have already done for sure. They have shown very clearly how mistaken is to adopt an anthropomorphic, or patronising, attitude towards the physiology of *Arenicola*, as if the worm were merely a mammal *manqué*.

Looking back over this lecture, I find the everlasting recurrence of the same refrain: "we can't be sure yet—we don't yet know enough". I hope very much that you have not been bored by its repetition. To end on a more cheerful note, it need only be pointed out that all of the problems which puzzle us at present are soluble, and the material is waiting, in generous abundance, right outside our doors.

SUMMARY

The lugworm is adapted, not so much to an environment as to a way of life.

The ordinary, day-to-day life of the lugworm is reviewed, as a basis for the discussion of its adaptations. The worm generally lives in a burrow of characteristic form, and for most of the time it carries out a regular rhythmic sequence of movements (the Normal Cyclical Pattern), determined by certain spontaneous pacemakers and serving to integrate its various necessary activities. The N.C.P. is seen in its most typical form when the burrow is covered over by water. It can be modified to incorporate a method of aerial respiration under low-tide conditions, or as a periodic "testing" mechanism if the animal should be trapped in a limited volume of foul water. The N.C.P. is part of the worm's innate organisation, and clearly adapted to its way of life. In special circumstances, the worm carries out alternative behaviour sequences, apparently unrelated to the N.C.P.

The worm's body is divided into regions by local modifications of the metameric segmental plan. The functional significance of some of these regional differentiations is clear. The tail is a means of communicating with the sand surface in comparative safety, and the parapodia at the two ends of the trunk are divergently specialised in accordance with different types of movement. Certain other differentiations (distribution along the body of gills and nephridia, variation in the course of the efferent branchial vessels) can perhaps be explained as adapted to the headward water stream which the worm drives through its burrow, but in these cases the explanations, though superficially plausible, are unsupported by positive experimental evidence.

The properties of *Arenicola* haemoglobin are considered as an example of physiological adaptation. The peculiarities of the oxygen dissociation curve are hard to understand if we assume that the worm is trying to do with its haemoglobin the same kind of things that we do with ours, and one may seriously doubt whether the pigment ever plays a part in oxygen transport. Recent suggestions that the haemoglobin serves, among other functions, to protect the worm against two poisons—oxygen excess and hydrogen sulphide—offer explanations of the peculiarities of the oxygen dissociation curve, of the considerable individual variations in haemoglobin concentration, and of the great development of haematopoietic tissues in the body.

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