SOME DIFFICULTIES IN THE LIFE OF AQUATIC INSECTS.[1]

WE understand insects to be animals of small size, furnished with a hard skin and six legs, breathing by branched air-tubes, and commonly provided in the adult condition with wings. The animals thus organized are pre-eminently a dominant group, as is shown by the vast number of the species and individuals, their universal distribution, and their various habitat.

The insect type, like some fruitful inventions of man—paper or lithography, for instance—has proved so successful that it has been found profitable to adapt it to countless distinct purposes. I propose to consider one only of its infinitely varied adaptations, viz. its adaptation to aquatic life.

There are insects which run upon the earth, insects which fly in the air, and insects which swim in the water. The same might be said of three other classes of animals—the three highest—viz. mammals, birds, and reptiles. But insects surpass all other classes of animals in the variety of their modes of existence. Owing to their small size and hard skin, they can burrow into the earth, into the wood of trees, or into the bodies of other animals. There are some insects which can live in the water, not as the mammal, bird, or reptile does, coming up from time to time to breathe, but constantly immersed, like a fish. This is the more remarkable because insects are, as a class, air-breathers. Air-tubes or tracheæ, branching tubes, whose walls are stiffened by spiral threads, supply all the tissues of the body with air. That such an animal should be hatched in water, and live almost the whole of its life immersed, a thing which actually happens to many insects, is a matter for surprise, and implies many modifications of structure, affecting all parts of the body.

The adaptation of insects to aquatic conditions seems to have been brought about at different times, and for a variety of distinct purposes. Many Dipterous larvæ burrow in the earth. Some of these frequent the damp earth in the neighbourhood of streams; others are found in earth so soaked with water that it might almost be called mud, though they breathe by occasionally taking in atmospheric air. In yet more specialized members of the same order we find that the larva inhabits the mud at the bottom of the stream, and depends for its respiration entirely upon oxygen dissolved in the water. The motive is usually that the larva may get access to the decaying vegetable matter found in slow streams, but some of these larvæ have carnivorous propensities.

Other insects merely dive into the water, coming up from time to time to breathe, or skate upon the surface.

Nearly every order of insects contains aquatic forms, and the total number of such forms is very large. I believe that all are modifications of terrestrial types, and it is probable that members of different families have often betaken themselves to the water independently of one another.

The difficulties which aquatic insects have to encounter begin with the egg. It is in most cases convenient that the egg should be laid in water, though this is not indispensable, and the winged, air-breathing fly is, as a rule, ill-fitted for entering water. Some insect-eggs hatch if they are merely scattered, like grains of sand, over the bottom of a stream, but others must be laid at the surface of the water, where they can gain a sufficient supply of oxygen. If the water is stagnant, it will suffice if the eggs are buoyant, like those which compose the egg-raft of the gnat, but this plan would hardly answer in running streams, which would carry light, floating eggs to great distances, or even sweep them out to sea. Moreover, floating eggs are exposed to the attacks of hungry creatures of various kinds, such as birds or predatory insect larvæ. These difficulties have been met in the cases of a number of insects by laying the eggs in chains or strings, and mooring them at the surface of the water. The eggs are invested by a gelatinous envelope, which swells out, the moment it reaches the water, into an abundant, transparent mucilage. This mucilage answers more than one purpose. In the first place it makes the eggs so slippery that birds or insects cannot grasp them. It also spaces the eggs, and enables each to get its fair share of air and sunlight. The gelatinous substance appears to possess some antiseptic property, which prevents water-moulds from attacking the eggs; for, long after the eggs have hatched out, the transparent envelope remains unchanged. The eggs of the frog, which are laid in the stagnant water of ditches or ponds, float free at the surface, and do not require to be moored. The eggs of many snails are laid in the form of an adhesive band, which holds firmly to the stem or leaf of an aquatic plant. Some insects, too, lay their eggs in the form of an adhesive band. In other cases the egg-chain is moored to the bank by a slender cord.

The common two-winged fly, Chironomus, lays its eggs in transparent cylindrical ropes, which float on the surface of the water. During the summer months these egg-ropes, which are nearly an inch in length, may readily be found on the edges of a stone fountain in a garden, or in a water-trough by the side of the road. The eggs are arranged upon the outside of the rope in loops, which bend to right and left alternately, forming sinuous lines upon the surface. Each egg-rope is moored to the bank by a thread, which passes through the middle of the rope in a series of loops, and then returns in as many reversed and overlapping loops, so as to give the appearance of a lock-stitch. The thread is so tough that it can be drawn out straight with a needle without breaking. If the egg-rope is dipped into boiling water, the threads become apparent, but in the natural state they are invisible, owing to their transparency. The mucilage is held together by the threads interwoven with the mucilage. The loops can be straightened without injury until the length of the rope is almost doubled. If stretched beyond this point the threads become strained, and do not recover their original shape when released. By means of these threads, firmly interwoven with the mucilage of the egg-rope, the whole mass of many hundreds of eggs is firmly moored, yet so moored that it floats without strain, and rises or falls with the stream. The eggs get all the sun and air which they require, and neither predatory insects, nor birds, nor water-moulds, nor rushing currents of water, can injure them.

The eggs of the caddis-fly are laid in larger ropes, which, in some species, are very beautiful objects, owing to the grass-green colour of the eggs. The egg-raft of the gnat, which has often been described, is well suited to flotation in stagnant water, and is freely exposed to the air, a point of unusual importance in the case of an insect which in all stages of growth seems to need the most efficient means of respiration, and whose eggs are usually laid in water of very doubtful purity. The lower or submerged end of each egg opens by a lid, and through this opening the larva at length escapes.

The eggs of water-haunting insects are in many ways particularly well suited for the study of development. The eggs of Chironomus, for instance, can always be procured during the summer months. They are so transparent as to admit of examination under high powers of the microscope as living objects, and as they require no sort of preparation, they may be replaced in the water after each examination to continue their development. This saves all trouble in determining the succession of the different stages—a point which usually presents difficulties to the embryologist. The whole development of the egg of Chironomus is completed in a few days (three to six, according to temperature), and it is therefore an easy matter to follow the process throughout with the help of three or four chains of eggs.

When the larvæ are hatched, and escape into the water, new difficulties arise. Some have to seek their food at the surface of the water, and must yet be always immersed, others live upon food which is only to be found in rapid streams, and these run serious risk of being swept away by the rush of water. All need at least a moderate supply of oxygen, which has either to be drawn from the air at the surface, or extracted from the water by special organs. The difficulty of breathing is, of course, greatly increased when the larva seeks its food at the bottom of foul streams, as is the case with certain Diptera. The larva of Chironomus, for example, feeds upon vegetable matter, often in a state of decay, which is obtained from the mud at the bottom of slow streams, and in this mud the larva makes burrows for itself, cementing together all sorts of materials by the secretion of its salivary glands, drawn out into fine silken threads. The burrows in which the larva lives furnish an important defence against fishes and other enemies, but they still further increase the difficulty of procuring a supply of air. Hence, the larva frequently quits its burrow, especially by night, and swims towards the surface. At these times it loops its body to and fro with a kind of lashing movement, and is thus enabled to advance and rise in the water. From the well-aërated water at the surface of the stream it procures a free supply of oxygen,

[1] Evening Discourse, delivered before the British Association, Cardiff, 1891, by L. C. Miall, Professor of Biology in the Yorkshire College.

which becomes dissolved in the abundant blood of the larva. Four delicate tubes filled with blood, which are carried upon the last segment of the body, are believed to be especially intended for the taking up of dissolved oxygen. The tracheal system is rudimentary and completely closed, and hence gaseous air cannot be taken into the body. The dissolved oxygen, procured with much exertion and some risk, must be stored up within the body of the larva, and used with the greatest economy. It is apparently for this reason that the larva of Chironomus contains a blood-red pigment, which is identical with the hæmoglobin of vertebrate animals. The hæmoglobin acts in the Chironomus larva as it does in our own bodies, as an oxygen-carrier, readily taking up dissolved oxygen, and parting with it gradually to the tissues of the body.

It is instructive to notice that only such Chironomus larvæ as live at the bottom and burrow in the mud possess the red hæmoglobin. Those which live at or near the surface have colourless blood, and a more complete, though still closed, tracheal system. The larva of the carnivorous Tanypus, which is found in the same streams, but does not burrow, has a much more complete tracheal system, and only enough hæmoglobin to give a pale red tint to the body. The larva of the gnat again, which has a large and open tracheal system, and in all stages of growth inhales gaseous air, has no hæmoglobin at all. A list of the many animals of all kinds which contain hæmoglobin, shows that for some reason or another each of them requires to use oxygen economically. Either the skin is thick, and the respiratory surface limited, or they are inclosed in a shell, or they burrow in earth or mud. We might expect to find that hæmoglobin would always be developed in the blood of animals whose respiration is rendered difficult in any of these ways, but any such expectation would prove to be unfounded, and there are many animals whose mode of life renders it necessary that oxygen should be stored and economically used, which contain no hæmoglobin in their blood. Hence, while we have a tolerably satisfactory reason for the occurrence of hæmoglobin in a number of animals whose respiratory surface is limited, and whose surroundings make it a matter of difficulty to procure a sufficient supply of oxygen, we have to admit that many similar animals under the same conditions manage perfectly well without hæmoglobin. Such admission is not a logical refutation of the explanation. I might fairly put forward the baldness of mankind as at least the principal reason for wearing wigs, and this explanation would not be impaired by any number of cases of bald men who do not wear wigs. The fact is that the respiratory needs, even of closely allied animals, vary greatly, and further, there are more ways than one of acquiring and storing up oxygen in their bodies.

Either the storage-capacity for oxygen of the Chironomus larva is considerable, or it must be used very carefully, for the animal can subsist long without a fresh supply. I took a flask of distilled water, boiled it for three-quarters of an hour, closed it tight with an india-rubber bung, and left it to cool. Then six larvæ were introduced, the small space above the water being at the same time filled up with carbonic acid. The bung was replaced, and the larvæ were watched from day to day. Four of the larvæ survived for forty-eight hours, and one till the fifth day. Two of them changed to pupæ. Nevertheless, the water was from the first exhausted of oxygen, or nearly so.

The Chironomus larva is provided with implements suited to its mode of life. The head, which is extremely small and hard, carries a pair of stout jaws, besides a most complicated array of hooks, some fixed, some movable. The use of these minute appendages cannot always be assigned, but some of them are apparently employed to guide the silky threads which issue from the salivary glands. The first segment behind the head carries a pair of stumpy legs, which are set with many hooks. These are mainly used in progression, and help the larva to hitch itself to and fro in its burrow. A similar, but longer pair of hooked feet is found at the end of the body. This hinder pair serves to attach the animal to its burrow when it stretches forth in search of food.

Creeping aquatic larvæ, such as Ephydra, possess several pairs of legs in front of the last pair, but the burrowing species, such as caddis-worms, agree with Chironomus, not only in their mode of life, but also in the reduction of the abdominal legs to a single pair, which are conspicuously hooked.

The larval head in this, as in many other aquatic insects, is far smaller and simpler than that of the fly. The larval head is little more than an implement for biting and spinning, by no means such a seat of intelligence as it is in higher animals. In Chironomus it contains no brain; the eyes are mere specks of pigment, and the antennæ are insignificant. But the head of the fly incloses the brain, and bears elaborate organs of special sense—many-facetted eyes, and in the male beautiful plumed antennæ. This difference in size and complexity probably explains the fact that the head of the fly is not developed within the larval head, but in the thorax. It is only at the time of pupation that it becomes everted, and its appendages assume the position which they are ultimately intended to occupy.

At length the Chironomus wriggles out of the larval skin, and is transformed into a pupa. It no longer requires to feed, and the mouth is completely closed. It is equally unable to burrow, and usually lies on the surface of the mud. Two tufts of silvery respiratory filaments project from the fore-end of the body just behind the future head, and these wave to and fro in the water, as the animal alternately flexes and extends its body. At the tail-end are two flaps, fringed with stout bristles, which form a kind of fan. The pupa virtually consists of the body of the fly, inclosed within a transparent skin. The organs of the fly are already complete externally, and even in microscopic detail they very closely resemble those of the perfect animal. These parts are, however, as yet very imperfectly displayed. The wings and legs are folded up along the sides of the body, and are incapable of independent movement. For two or three days there is no outward change, except that the pupa, which originally had the blood-red colour of the larva, gradually assumes a darker tint. The tracheal system, which was quite rudimentary in the larva, but is now greatly enlarged, becomes filled with air, secreted from the water by the help of the respiratory tufts, and the pupa floats at the surface. At last the skin of the back splits, the fly extricates its limbs and other appendages, pauses for a moment upon the floating pupa-case, as if to dry its wings, and then flies away.

This fly is a common object on our window panes, and would be called a gnat by most people. It can be easily distinguished from a true gnat by its habit of raising the fore-legs from the ground when at rest. It is entirely harmless, and the mouth-parts can neither pierce nor suck. Like many other Diptera, the flies of Chironomus associate in swarms, which are believed in this case to consist entirely of males. The male fly has plumed antennæ with dilated basal joints. In the female fly the antennæ are smaller and simpler, as well as more widely separated.

In brisk and lively streams another Dipterous larva may often be found in great numbers. This is the larva of Simulium, known in the winged state as the sand-fly. The Simulium larva is much smaller than that of Chironomus, and its blood is not tinged with red. The head is provided with a pair of ciliary organs, fan-like in shape, consisting of many longish filaments, and borne upon a sort of stem. The fringed filaments are used to sweep the food into the mouth. The larva of Simulium subsists entirely upon microscopic plants and animals. Among these are great numbers of Diatoms, and the stomach is usually found half full of the flinty valves of these microscopic plants. The Simulium larva seeks its food in rapid currents of water, and a brisk flow of well-aërated water has apparently become a necessity to it. If the larvæ are taken out of a stream and placed in a vessel of clear water, they soon become sluggish, and in warm weather do not survive very long. It matters little, however, to the larvæ whether the water in which they live is pure or impure; and streams which are contaminated with sewage often contain them in great abundance. There are no externally visible organs of respiration, but the skin is supplied by an abundant network of fine tracheal branches, which, no doubt, take up oxygen from the well-aërated water in which the animal lives. From this network at the surface, branches pass to supply all the internal organs. The Simulium larva is found upon aquatic weeds, and the pair of hind-feet, which in Chironomus were shaped so as to enable the larva to hold on to its burrow, here become altered, so as to furnish a new means of attachment. The two feet are completely united into one. The two clusters of hooks found in the Chironomus larva form now a circular coronet, and the centre of the inclosed space becomes capable of being retracted by means of muscles which are inserted into it from within. The larva is thus enabled to adhere to the smooth surface of a leaf, holding on by its sucker, which is, no doubt, aided by the circle of sharp hooks. Efficient as this adhesive organ undoubtedly is, it must be liable to derangement by occasional accidents, as, for instance, if there should be a sudden rush of water of unusual violence, or if the larva should be obliged to quit its hold in order to avoid some dangerous enemy. In the case of such an accident it is not easy to see how it will ever recover its footing. Swept along in a rapid current, we might suppose that there would be but a slender probability of its ever finding itself favourably placed for the application of its sucker and hooks. But such emergencies have been carefully provided for. The salivary glands, or silk-organs, which the Chironomus larva uses in weaving the wall of its burrow, furnish to the Simulium larva long mooring-threads, by means of which it is anchored to the leaf upon which it lives. Even if the larva is dislodged, it is not swept far by the stream, and can haul itself in along the mooring-thread in the same way that a spider or a Geometer larva climbs up the thread by which, when alarmed, it descended to the ground.

When the time for pupation comes, special provision has to be made for the peculiar circumstances in which the whole of the aquatic life of the Simulium is passed. An inactive and exposed pupa, like that of Chironomus, may fare well enough on the soft muddy bottom of a slow stream, but such a pupa would be swept away in a moment by the currents in which Simulium is most at home. When the time of pupation draws near, the insect constructs for itself a kind of nest, not unlike in shape the nest of some swallows. This nest is glued fast to the surface of a water-weed. The salivary glands, which furnished the mooring-threads, supply the material of which the nest is composed. Sheltered within this smooth and tapering case, whose pointed tip is directed up-stream, while the open mouth is turned down-stream, the pupa rests securely during the time of its transformation.

When the pupa-case is first formed, it is completely closed and egg-shaped, but, when the insect has cast the larval skin, one end of the case is knocked off, and the pupa now thrusts the fore-part of its body into the current of water. The respiratory filaments, which project immediately behind the future head, just as in Chironomus, draw a sufficient supply of air from the continually changed water around. The rings of the abdomen are furnished with a number of projecting hooks, which are able to grasp such objects as fine threads. The interior of the cocoon is felted by a number of silken threads, and by means of these the pupa gets an additional grip of its case. If it is forcibly dislodged, a number of the silken threads are drawn out from the felted lining of the case. The fly emerges into the running water, and I do not know how it manages to do so without being entangled in the current of water, and swept down the stream. The pupa-skin splits open just as it does in Chironomus, but remains attached to the cocoon.

The larva of the gnat is perhaps more familiar to naturalists of all kinds than any other aquatic Dipterous insect. The interesting description, and, above all, the admirable engravings, of Swammerdam, now more than two hundred years old, are familiar to every student of Nature.

The larva, when at rest, floats at the surface of stagnant water. Its head, which is provided with vibratile organs suitable for sweeping minute particles into the mouth, is directed downwards, and, when examined by a lens in a good light, appears to be bordered below by a gleaming band. There are no thoracic limbs. The hind-limbs, which were long and hooked in the burrowing Chironomus larva, and reduced to a hook-bearing sucker in Simulium, now disappear altogether. A new and peculiar organ is developed from the eighth segment of the abdomen. This is a cylindrical respiratory siphon, traversed by two large air-tubes, which are continued along the entire length of the body, and supply every part with air. The larva ordinarily rests in such a position that the tip of the respiratory siphon is flush with the surface of the water, and, thus suspended, it feeds incessantly, breathing uninterruptedly at the same time. When disturbed, it leaves the surface by the sculling action of its broad tail. Once below the surface, it sinks slowly to the bottom by gravity alone, which shows that the body is denser than the water. We have, therefore, to explain how it is enabled to float at the surface when at rest. The larva does not willingly remain below for any length of time. It rises by a jerking movement, striking rapid blows with its tail, and advancing tail foremost. When it reaches the top, it hangs as before, head downwards, and resumes its feeding operations.

In order to explain how the larva hangs from the surface against gravity, I must trouble you with some account of the properties of the surface-film of water. You will readily believe that I have nothing new to communicate on this subject, and I venture to show you a few very simple experiments, merely because they are essential to the comprehension of what takes place in the gnat.[1]

In any vessel of pure water, the particles at the surface, though not differing in composition from those beneath, are nevertheless in a peculiar state. I will not travel so far from the region of natural history as to offer any theoretical explanation of this state, but will merely show you experimentally that there is a surface-film which resists the passage of a solid body from beneath. [Mensbrugghe's float shown.] You see (1) that the float is sufficiently buoyant to rise well out of the water; (2) that, when forcibly submerged, it rises with ease through the water as far as the surface-film; (3) that it is detained by the surface-film, and cannot penetrate it. The wire pulls at the surface-film and distorts it, but is unable to free itself. In the same way the surface-film resists the passage of a solid body which attempts to penetrate it from above. This will be readily seen if we throw a loop of aluminium wire upon the surface of water. [Experiment shown.] The loop of wire floats about like a stick of wood. Aluminium is, of course, much lighter than iron, but the floating of this little bar does not mean that it has a lower density than that of water. If the bar is once wetted, it sinks to the bottom and remains there. Even a needle may, with a little care, be made to float upon the surface of perfectly pure water. Still more readily can a piece of metallic gauze be made to float on water. [Experiment shown.] Air can pass through the meshes with perfect ease; water also can pass through the meshes with no visible obstruction. But the surface-film, bounding the air and water, is entirely unable to traverse even meshes of appreciable size. These simple experimental results will enable us to appreciate certain facts of structure, which would otherwise be hard to understand, and which have been wrongly explained by naturalists of the greatest eminence, to whom the physical discoveries of this century were unknown.

We may now try to answer three questions about the larva of the gnat, viz.:—

(1) How is it able to break the surface-film when it swims upwards?

(2) How is it able to remain at the surface without muscular effort, though denser than water?

(3) How is it able to leave the surface quickly and easily when alarmed?

The tip of the respiratory siphon is provided with three flaps, two large and similar to one another, the third smaller and differently shaped. These flaps can be opened or closed by attached muscles. When open, they form a minute basin, which, though not completely closed, does not allow the surface-film of water to enter. When closed, the air within the siphon is unable to escape. At the time when the larva rises to the surface, the pointed tips of the flaps first meet the surface-film, and adhere to it. The attached muscles then separate the flaps, and in a moment the basin is expanded and filled with air. The surface-film is now pulling at the edges of the basin, and the pull is more than sufficient to counterbalance the greater density of the body of the larva, which accordingly hangs from the surface without effort. When the larva is alarmed, and wishes to descend, the valves close, their tips are brought to a point, and the resisting pull of the surface-film is reduced to an unimportant amount. [Living larvæ shown by the lantern.]

Swammerdam found it necessary, in explaining the flotation of the larva of the gnat to suppose that the extremity of its siphon was supplied with an oily secretion which repelled the water. No oil-gland can be discovered here or elsewhere in the body of the larva, and indeed no oil-gland is necessary. The peculiar properties of the surface-film explain all the phenomena. The surface-film is unable to penetrate the fine spaces between the flaps for precisely the same reason that it is unable to pass through the meshes in a piece of gauze.

After three or four moults the larva is ready for pupation. By this time the organs of the future fly are almost completely formed, and the pupa assumes a strange shape, very unlike that of the larva.

At the head-end is a great rounded mass, which incloses the wings and legs of the fly, beside the compound eyes, the mouth-parts, and other organs of the head. At the tail-end is a pair

1 A number of other experiments, illustrating the properties of the surface-film of water, are described by Prof. Boys in his delightful book on "Soap Bubbles."

of flaps, which form an efficient swimming-fan. The body of the pupa, like that of the larva, is abundantly supplied with air-tubes, and a communication with the outer air is still maintained, though in an entirely different way. The air-tubes no longer open towards the tail, as in the larva, but towards the head. Just behind the head of the future fly is a pair of trumpets, so placed that in a position of rest the margins of the trumpets come flush with the surface of the water. Floating in this position, the pupa remains still, so long as it is undisturbed, but if attacked by any of the predatory animals which abound in fresh waters, it is able to descend by the powerful swimming movements of its tail fin.

Not that the descent is without its difficulties. The pupa is not like the larva, denser than water, but buoyant. There are two respiratory tubes in the pupa, whereas there is only one in the larva, and to these two tubes the surface-film clings with a tenacity of which only experiment can give an adequate idea. Will you allow me to give you a little more borrowed physics?

If we take a solid body, capable of being wetted by water, and place it in water, the surface-film will adhere to the solid. If the solid is less dense than the water, it will float with part of its surface out of the water. Under such circumstances the surface-film will be drawn upwards around the solid, and will therefore pull the solid downwards. But if the solid is denser than the water, the surface-film around the solid will be pulled downwards, and will pull the solid upwards. Suppose that a solid of the same density as water floats with part of its surface in contact with air, and that weights are gradually added to it. The result will be that the surface of the water around the upper edge of the solid will become more and more depressed. The sides of the depression will take a more vertical position, until at last the upward pull of the film becomes unable to withstand further increase of weight. If this point is passed, the solid will sink. Before this point is attained, we shall have the solid, though denser than water, kept at the surface by the pull of the surface-film.

This state of things may be illustrated by a model. [Float with glass tube attached to its upper surface.] You will readily see that the float has to be weighted appreciably in order to break the connection of the tube with the surface-film. Now the pupa of the gnat has a pair of tubes which are in like manner attached to the surface of the water. When it requires to descend, the pull of the surface-film would undoubtedly be considerable. Adding weight to the body is, of course, impossible, and a great exertion of muscular force would be wasteful of energy, even if it could be put forth. The gnat deals with its difficulty in a neater way than this, and saves its muscular power for other occasions. Let me show you a method of freeing the float from the surface, which was suggested by observation of what was seen in the pupa of the gnat. A thread wetted with water is drawn over the mouth of each tube. It cuts the connection with the surface, and the float, loaded so as to be denser than water, goes down at once. Meinert has described a pencil of hairs which appear to perform the same office for the pupa of the gnat. The hairs draw a film of water over the open mouth of each respiratory tube, and muscular contraction, used moderately and economically, does the rest. When the pupa again comes to the surface the tubes are overspread by a glistening film of water. This is partially withdrawn by a movement of the hairs, so that a chink appears by which air can be slowly renewed. When the insect is completely tranquil, the hairs appear to withdraw more completely, and the tube suddenly becomes free of all film. The act of opening or closing the film is so rapid—like the wink of an eye—that I cannot pretend to have observed more than the closed tube, the slightly open tube, and then the sudden change to a completely open condition. [Living pupæ shown by the lantern.]

Another Dipterous larva described and admirably figured by Swammerdam is the larva of Stratiomys, a larva which, as the structure of the fly shows, belongs to an altogether different group from Chironomus, Simulium, or the gnat. Though only remotely connected with the gnat in the systems of zoologists, the Stratiomys larva has learned the same lesson, and is equally well fitted to take advantage of the peculiar properties of the surface-film. The tail-end of the Stratiomys larva is provided with a beautiful coronet of branched filaments. When this coronet is extended, it forms a basin open to the air and impervious to water, by reason of the fineness of the meshes between the component filaments. Were the larva provided with a basin of the same proportions formed out of continuous membrane, it might float and breathe perfectly well, but the old difficulty would come back, viz. that of freeing itself neatly and quickly when some sudden emergency required the animal to leave the surface. As it is, the plumed filaments collapse and their points approach; the side-branches are folded in, and the basin is in a moment reduced to a pear-shaped body, filled with a globule of air, and reaching the surface of the water only by its pointed extremity. Down goes the Stratiomys larva at the first hint of danger, swimming through the water with swaying and looping movements, somewhat like those of Chironomus. When the danger is past, it ceases to struggle, and floats again to the surface. The pointed tip of its tail-fringe pierces the surface-film, the filaments separate once more, and the floating basin is restored.

The larva of Stratiomys is extremely elongate. The length of its body has evidently some relation to the mode of life of the larva, but none at all to that of the fly which is formed within it. The pupa is so much smaller than the larva as to occupy only the fore-part of the space within the larval skin.[1] The interval becomes filled with air, and during the pupal stage the animal floats at the surface within the empty larval skin.

Stratiomys, both in its larval and pupal states, floats at the surface of the water. The larva can descend into the water when attacked, but the pupa is too buoyant, and too much encumbered by its outer case, to execute any such manœuvre. Provision has accordingly to be made for the protection of the helpless pupa against its many enemies. It is probable that hungry insects and birds mistake the shapeless larval skin, floating passively at the surface, for a dead object. The considerable space between the outer envelope, or larval skin, and the body of the pupa may keep off others, for the first bite of a Dytiscus or dragon-fly larva would be disappointing. Still further security is gained by the texture of the larval skin itself. The cuticle consists of two layers. The inner is comparatively soft and laminated, while the outer layer is impregnated with calcareous salts, and extremely hard. The needful flexibility is obtained by the subdivision of the hard outer layer. Seen from the surface, it is broken up into a multitude of hexagonal fields, each of which forms the base of a conical projection, reaching far into the softer layer beneath. The conical shape of these calcareous nails allows a certain amount of bending of the cuticle, while the whole exposed surface is protected by an armour, in which even the pointed mandibles of a Dytiscus larva can find no effective chink.

The larva and pupa of the Dipterous fly, *Ptychoptera paludosa*, exhibit some interesting adaptations of the tracheal system to unusual conditions. The larva is found in muddy ditches, where it buries itself in the black ooze to a depth of an inch or two. Here, of course, it can procure no oxygen, either gaseous or dissolved. When it requires a fresh supply, it must reach the surface with part of its body, and to enable it to do so with the least possible exertion, the tail-end of the body is made telescopic, like that of another and still more familiar Dipterous larva, Eristalis. The last segments are drawn out very fine, and are capable of a very great amount of retraction or expansion. No visible opening for the admission of air has been discovered, nor do the hairs form a floating basin, as in the Stratiomys larva. The larva may be often seen lying just beneath the surface, which is broken by the tip of the tail. Whether air can be admitted here by some very minute orifice, or whether it is renewed by the exchange of gases through a thin membrane, I cannot as yet venture to say. In shallow water the larva may be occasionally found lying on or in the mud, and stretching out its long tail to the surface. In deeper water, it often floats at the surface.

Two tracheal trunks run along the whole length of the body, including the slender tail, where they are extremely convoluted and unbranched. Towards the middle of the body the tracheæ become greatly enlarged in the centre of each segment, the intervening portions, from which many branches are given off, being comparatively narrow. Each tube, therefore, resembles a row of bladders connected by small necks. A cross-section shows that the tubes are not cylindrical, but flattened, and that, while the lower surface is stiffened by the usual parallel thickenings, the upper surface is thrown into two deep, longitudinal furrows, so that it is readily inflated, becoming circular in section, and readily collapses again when the air is expelled. It seems likely

[1] So singular is the disproportion between the larva and the pupa that some naturalists have actually described the latter as a parasite (Westwood's "Mod. Classification of Insects," vol. ii. p. 532).

that the buoyancy of the larva can thus be regulated, and a larger or smaller quantity of air taken in as desired.

The pupa has a pair of respiratory tubes, which are carried, not on the tail, but on the thorax, close behind the head. One of these tubes is very long, the other very short. The long tube is twice as long as the body, and tapers very gradually to its free tip. Here we find a curious radiate structure, rather like the teeth of a moss-capsule, which seems adapted for opening and closing. There is, however, no orifice which the most careful scrutiny has succeeeded in discovering. A delicate membrane extends between the teeth, and prevents any passage inwards or outwards of air in mass. The tube incloses a large trachea, the continuation of one of the main tracheal trunks. This is stiffened by a spiral coil, but at intervals we find the coil deficient, while the wall of the tube swells out into a thin bladder. However the tube is turned, a number of these bladders come to the surface. As the pupa lies on the surface of the mud, the filament floats on the top of the water, and the air is renewed without effort through the thin-walled bladders.

Why should the position of the respiratory organs be changed from the tail-end in the larva to the head-end in the pupa? Chironomus, the gnat, Corethra, and many other aquatic insects exhibit the same phenomenon. Evidently there must be some reason why it is more convenient for the larva to take in air by the tail, and for the pupa to take in air by the head. Let us consider the case of the larva first. Where it floats from the surface, or pushes some part of its body to the surface, it is plain that the tail must come to the top and bear the respiratory outlet, for the head bears the mouth and mouth-organs, and must sweep to and fro in all directions, or even bury itself in the mud in quest of food. To divide the work of breathing and feeding between the opposite ends of the body is of obvious advantage, for the breathing can be done best at the top of the water, and the feeding at the bottom, or at least beneath the surface. Such considerations seem to have fixed the respiratory organs at the tail of the larva. Why, then, need this arrangement be reversed when the insect enters the pupal stage? There is now no feeding to be done, and it surely does not signify how the head is carried. Why should not the pupa continue to breathe like the larva, by its tail, instead of developing a new apparatus at the opposite end of its body, as if for change's sake? Well, it does not appear that, so far as the pupa itself is concerned, any good reason can be given why the larval arrangement should not continue. But a time comes when the fly has to escape from the pupa-case. The skin splits along the back of the thorax, and here the fly emerges, extricating its legs, wings, head, and abdomen from their close-fitting envelopes. The mouth-parts must be drawn backwards out of their larval sheaths, the legs upwards, and the abdomen forwards, so that there is only one possible place of escape, viz. by the back of the thorax, where all these lines of movement converge. If, then, the fly must escape by the back of the thorax, the back of the thorax must float uppermost during at least the latter part of the pupal stage. Otherwise the fly would emerge into the water instead of into the air. Granting that the back of the thorax must float uppermost in the pupal condition, it is clear that here the respiratory tubes must be set.

I need hardly speak of the many insects which run and skate on the surface of the water in consequence of the peculiar properties of the surface-film. They are able to do so, first, by reason of their small size; secondly, because of the great spread of their legs; and thirdly, on account of the fine hairs with which their legs are provided. The adhesion of the surface-film is measured by the length of the line of contact, and accordingly the multiplication of points of contact may indefinitely increase the support afforded by the surface of the water.

In the case of very small insects, it becomes possible, not only to run on the surface of the water, but even to leap upon it, as upon a table. This is particularly well seen in one of the smallest and simplest of all insects—the little black Podura, which abounds in sheets of still water. The minute and hairy body of the Podura is incapable of being wetted, and the insect frisks about on the silvery surface of a pond, just as a house-fly might do on the surface of quicksilver. This is all very well so long as the Podura is anxious only to amuse itself, or move from place to place, but it has to seek its food in the water, and, indeed, the attractiveness of a sheet of water to the Podura lies mainly in the decaying vegetation far below the surface. But if the insect is thus incapable of sinking below the surface, how does it ever get access to its submerged food? I have endeavoured to arrive at the explanation of this difficulty by observation of Poduras in captivity. If you place a number of Poduras in a beaker half full of water, they are wholly unable to sink. They run about and leap upon the surface, as if trying to escape from their prison, but sink they cannot. I have chased them about with a small rod until they became excited and much alarmed, but they were wholly unable to descend. Even when large quantities of alcohol were added to the water, the dead bodies of the Podura are seen floating at the top, almost as dry as before. It is only when they are placed upon the surface of strong alcohol that the dead bodies become wetted, and after a considerable time are seen to sink. How, then, does the Podura ever descend to the depths where its food is found?

I found it an easy matter to make a ladder, by which the Poduræ could leave the upper air. A few plants of duck-weed introduced into the beaker enabled them at pleasure to pull themselves forcibly through the surface-film, and climb down the long root hanging into the water like a rope. Once below the surface, the Podura, though buoyant, is enabled, by muscular exertion, to swim downwards to any depth.

Other aquatic insects, not quite so minute as the Podura, experience something of the same difficulty. A Gyrinus, or a small Hydrophilus, finds it no easy matter to quit the surface of the water, and is glad of a stem or root to descend by.

To leave our aquatic insects for a moment, we may notice the habit of creeping on the under-side of the surface-film, which is so often practised by leeches, snails, cyclas, &c. I find this is often described as creeping on the *air*, and some naturalists of the greatest eminence, speak of fresh-water snails as creeping "on the stratum of air in contact with the surface of the water."[1] The body of the animal is, nevertheless, wholly immersed during this exercise, as may be shown by a simple experiment. If Lycopodium powder is sprinkled over the water, the light particles are not displaced by the animal as it travels beneath. The possibility of creeping in this manner depends, not upon any "repulsion between the water and the dry surface of the body," to quote an explanation which is often given, but upon the tenacity of the surface-film, which serves as a kind of ceiling to the water-chamber below. The body of the leech is distinctly of higher specific gravity than the water, and falls quickly to the bottom, if the animal loses its hold of the surface-film. The pond-snails, however, actually float at the surface, and if disturbed, or made to retract their foot, they merely turn over in the water.

What is the result of all the expedients which have enabled air-breathing insects to overcome the difficulties of living in water? They have been successful, we might almost say too successful, in gaining access to a new and ample store of food. Aquatic plants, minute animals, and dead organic matter of all kinds abound in our fresh waters. Accordingly the species of aquatic insects have multiplied exceedingly, and the number of individuals in a species is sometimes surprisingly high. The supply of food thus opened out is not only ample, but in many cases very easy to appropriate. Accordingly the head of the larva degenerates, becomes small and of simple structure, and may be in extreme cases reduced to a mere shell, not inclosing the brain, and devoid of eyes, antennæ, and jaws. The organs of locomotion also commonly afford some indications of degeneration. Where the insect has to find a mate, and discover suitable sites for egg-laying, the fly at least must possess some degree of intelligence, keen sense-organs, and means of rapid locomotion. But some few aquatic insects, as well as some non-aquatic species which have found out an unlimited store of food, manage to produce offspring from unfertilized eggs, and to have these eggs laid by wingless pupæ or hatched within the bodies of wingless larvæ. The development of the winged fly, the whole business of mating, and even the development of the embryo within the egg, have thus, in particular insects, been abbreviated to the point of suppression. This is what I mean by saying that the pursuit of a new supply of food has in the case of certain aquatic insects proved even too successful. Abundant food, needing no exertion to discover or appropriate it, has led in a few instances to the almost complete atrophy of those higher organs and functions which alone make life interesting.

The degeneration of aquatic insects, however, very rarely reaches this extreme. In nearly all cases the pupa is succeeded by a fly, whose activity is in striking contrast to the sluggishness

[1] Semper's "Animal Life," Eng. trans., p. 205, and note 97.

of the larva. They differ, to the eye at least, almost as much as air differs from water.

Of the friends to whom I am indebted for help, I must specially name my fellow-worker, Mr. Arthur Hammond, who has communicated to me many results of his own observations, and has drawn most of the illustrations shown this evening. My colleague, Dr. Stroud, has very kindly arranged, and in some cases devised, the physical experiments which have been so helpful to us.

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