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ROYAL INSTITUTION OF GREAT BRITAIN.

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On the Metamorphoses of Insects. By Sir John Lubbock, Bart., F.R.S., M.R.I., Pres. Ent. Soc., V.P. Lin. Soc., V.P. Ethn. Soc., F.S.A.

The subkingdom Annulosa, to which insects belong, is divided into five classes, namely, Annelida, Crustacea, Arachnida, Myriopoda, Insecta.

The Annelida, or worms, have a body consisting of more or less numerous segments, but without any jointed appendages.

The Crustacea, or crabs and lobsters, have a jointed body, and each segment usually bears a pair of appendages. They are aquatic in their habits.

The Arachnida, or spiders, possess four pairs of legs; the body is divided into two parts, the cephalothorax and abdomen. The segments composing the abdomen bear no appendages. Spiders are aërial in their habits.

The Myriopoda, or centipedes, have a long body consisting of numerous segments, each of which bears a pair of legs.

The Insecta, or insects, have three pairs of legs. They are aërial in habits, and breathe by means of tracheæ or air-tubes, which ramify throughout the internal organs. The body is divided into three parts, the head, thorax, and abdomen.

In addition to the three pairs of legs, the thorax bears generally either two or four wings. The older naturalists collected the wingless forms into a special order—the Aptera; but more extended observations have shown that each of the large orders or groups into which insects are divided contains some apterous forms. The female glow-worm and the working ants are familiar examples of this.

But though the presence of wings is the rule, and the division of insects into orders is founded in great measure on the characters afforded by these important organs, still they are present only in the mature state of the animal, and no known insect is born with wings.

Not only in the absence of wings, but also generally in many other important points, the young insect differs from the mature form, and the changes which it goes through are known as metamorphoses. Entomologists have generally considered the life of all insects to be divisible into four well-marked periods—that of the egg, the larva or caterpillar, the pupa or chrysalis, and, finally, the imago or perfect insect. It is true that in some orders, as, for instance, the Coleoptera (beetles), Hymenoptera (bees), Lepidoptera (butterflies), and Diptera (flies), the larvæ differ much more from the perfect insects than is the case in others, as, for instance, the Orthoptera (grasshoppers) or Heteroptera (bugs); but even in these latter the stages were still supposed to be well marked,—that of the larva, by the entire absence of wings; that of the pupa, by the possession of rudimentary wings; finally, the perfect insect, by having perfect wings.

The lecturer then pointed out that, when the habits were alike, similar larvæ might be met with in very different families of insects. Thus, among beetles, the *Melolontha* (cockchafer), *Anobium* (death-watch), and *Chlamys* are very similar in their larva state, although they belong to perfectly distinct families of beetles—namely, the *Melolonthidæ*, *Ptinidæ*, and *Chrysomelidæ*.

The same fact holds good even in larvæ belonging to different orders of insects. Those larvæ which, in the words of Mr. Herbert Spencer, are "symmetrically related to the environment," and which either are surrounded by their food, or have it brought to them, are fat, legless, fleshy grubs or maggots. Such are almost all the larvæ of flies. So, again, the Hymenopterous larvæ are generally of this character: whether they inhabit other insects, like those of the ichneumons, or live inside galls, like those of the *Cynipidæ*, or are enclosed in cells and fed by the perfect insects, like those of the bees, practically any great deviation from that which may be looked upon as the normal type is unnecessary. The larvæ of beetles, on the contrary, are generally of a very different character. But there is one group, that of the weevils, which are internal feeders. The grub of a nut-weevil feeding inside a nut is under very similar conditions to those of a *Cynips*-larva in a gall, or an *Anthrax*-larva living parasitically in a bees' cell; and we accordingly find that these larvæ, though belonging to three different orders of insects, very closely resemble one another.

To this type belong most Hymenopterous larvæ; but there are two exceptional groups, the *Tenthredinidæ*, or sawflies, and the *Siricidæ*. The larvæ of the *Tenthredinidæ* feed, like those of butterflies, on leaves, and in the general form of the body, in the possession of three pairs of legs and several pairs of abdominal prolegs, they very closely resemble ordinary caterpillars, and differ extremely from the ordinary type of Hymenopterous larvæ. In the same manner the larvæ of the *Siricidæ*, which are wood-borers, possess thoracic legs, and closely resemble the larvæ of some wood-boring beetles.

From these facts it may be concluded that the form of a larva depends more on the conditions in which it lives than on the form which it will ultimately assume. But this is shown still more clearly in the case of *Sitaris*, a small beetle which is parasitic on a species of solitary bee (*Anthophora*), and the habits of which have been carefully observed and excellently described by a French naturalist, M. Fabre. The female *Sitaris*, which comes to maturity in August, never wanders far away from the sandy banks in which the *Anthophora* loves to burrow. At that time no Anthophoras are abroad, their period of maturity is not in autumn, but in spring; and consequently, though the bee is so necessary to the beetle, we are at once met with the remarkable fact that no perfect *Sitaris* ever saw one of the bees, and it is probable that no *Anthophora* has ever yet seen a *Sitaris*. The latter lays her eggs, which are about 2500 in number, in the burrow leading to the cell of the *Anthophora*. These eggs are hatched in September, and produce small, black, active larvæ, about $\frac{1}{25}$th of an inch in length, with four eyes, two rather long antennæ, and six well-

formed legs. But though evidently adapted for an active life, the young larvæ remain quiet among their empty egg-shells until the spring. Then the *Anthophora* comes to maturity, and as it passes out along the burrow the young larvæ spring upon it. The male bees, however, leave their cells about a month before the females; consequently the larva first finds itself on the male bee, from which, however, at the first opportunity it passes to the female. She, poor thing, unconscious of her misfortune, proceeds to excavate her burrow in the usual manner, constructs the usual cell, and fills it with honey. On the honey she lays her egg, but at this moment the larva of *Sitaris* springs on to the egg and floats on it, as on a raft. It then tears open the egg and devours it, thus at once destroying a rival, and making its first meal. As it has by this time been seven months without food, this its first food must be very welcome. But it is necessary on another account. The larva in its first form, though beautifully fitted for its mode of life, is quite unsuited to live on honey in a bees' cell. Hence a change of form is necessary. The increase of size produced by devouring the egg enables the larva to change its skin, and it now emerges in a form very different indeed from the last. The eyes have disappeared; the legs and antennæ are rudimentary. The mouth is so placed that when the larva floats on the honey it is just below the surface, while the spiracles are arranged along the back so as to be just above it. Lastly, the belly is very protuberant, and thus prevents the larva from rolling, in which case the spiracles might be choked by the honey, and the insect suffocated. After living from thirty-five to forty days in this condition, during which it increases very considerably in size, the larva ceases to feed, and contracts into an ovoid body, resembling in many respects the so-called pupa of a fly. Within this, as in a case, it forms a new skin, and takes on a fourth form not very unlike the second. After four or five weeks it changes again into a chrysalis, from which finally the perfect beetle emerges.

Here, then, we find, first, a remarkable change of form accompanying a change of habits, and, secondly, a case in which the life is divided into more than three well-marked stages. This phenomenon received from M. Fabre the name of hypermetamorphosis. For some time the cases of *Sitaris* and *Meloe* were looked on as exceptional; but in 1862 the attention of the lecturer was called to the question by observing a somewhat similar case in *Lonchoptera*, a genus of small flies. Moreover he found that in many species belonging to the Orthoptera and Hemiptera the stages were much less definite and more gradual than had hitherto been supposed.

In illustration of this he described the transformations of *Chloëon* (*Ephemeridæ*), and showed that the perfect form was attained through more than twenty changes of skin, each attended by a slight change of form. In its preparatory stages this insect lives in the water, but in the last two it becomes aërial. Sir John Lubbock had been so fortunate as to see more than once the passage from the aquatic to the aërial condition: the larva floated helplessly on the surface of the water; suddenly the skin burst, the insect sprang out

of the back of its own head, and fluttered away. The whole process occupied less than ten seconds.

The speaker in this case wished particularly to impress on his hearers, first, the gradual nature of the changes, and, secondly, that some of them have no reference to the form of the perfect insect, but are entirely of an adaptational character. Thus the young larva is born without branchiæ, and with two caudal appendages. It gradually acquires a thin tail and seven pairs of branchiæ; but the perfect insect has only two tails and no branchiæ. Thus, then, the changes which an insect undergoes are of two kinds, developmental and adaptational.

External forces act upon the larvæ as much as on the perfect insects. And we can thus understand the remarkable fact that some animals, which differ much when young, are very similar at maturity.

The speaker then entered into some theoretical considerations as to the nature and causes of metamorphoses, dividing the subject into three questions.

1st. How these changes of form might have originated.

2ndly. Why they are, in insects, so abrupt in their character; and

3rdly. Why the pupa condition, a period of approximate immobility, should intervene between the active larva and the still more active imago.

1. The changes of form depend on the early condition at which some insects quit the egg. There is reason to believe that all insects pass through the stage of fat, fleshy grubs, and subsequently acquire legs *. Some, however, are hatched in the first state, while others remain in the egg until they attain the second. In the former case additional changes are produced by the fact that external forces do not affect the larva in the same manner as the perfect insect; and thus there is a tendency to still greater differentiation.

2. The abruptness of the change is more apparent than real. The actual change itself is merely the withdrawal of the curtain, the casting of the old skin, by which the alterations which have perhaps been in preparation for days, or even weeks, are rendered visible. In fact there can be no great change in insects without a moult. Insects have no bones, and the muscles are attached to the skin, which therefore is necessarily hardened to afford them a solid and sufficient fulcrum. But it follows from this that no change of form can take place without a change of skin.

In *Chloëon* we have seen that each moult is accompanied by a slight change.

In caterpillars, on the contrary, there is little alteration during growth, and the changes are concentrated, so to say, on the last two moults. The advantage of this is obvious; the mouth, digestive, and other organs of the larva are very different from those of the perfect insect; and if the change from the one type to the other were gradual and slow, the insect would be liable to perish of starvation in the midst of plenty.

* See, for instance, Professor Huxley's admirable memoir on *Aphis*, in the 'Linnean Transactions.'

3. Similar considerations throw much light on the immobility of the pupa. The organs are altering so rapidly that they are unable to perform their functions. When the changes are gradual, as in Orthoptera, &c., there is no period of quiescence.

The speaker then pointed out the analogy between metamorphoses and the alternation of generations.

Many species of the lower animals are represented by two totally dissimilar forms ; but, so far as the speaker knew, no explanation of this remarkable phenomenon had yet been given.

Through the metamorphoses of insects, however, we get a clue. When an animal is born in a state so early that external forces act on it in one way, and on the perfect form in another, they tend to produce greater and greater differences between the two. As long as the external organs arrive at their mature form before the generative organs are fully developed, we have cases of metamorphosis; but if the reverse is the case, then alternation of generations is the result.

The same considerations explain why in alternation of generations the reproduction is almost invariably agamic in the one form. This is because impregnation requires the perfection both of external and internal organs ; and if the phenomenon arises, as has just been suggested, from the fact that the internal organs arrive at maturity before the external ones, impregnation cannot take place, and reproduction will only result in those species which have the power of agamic multiplication.

However this may be, insects offer every gradation between simple growth and that phenomenon which is known as alternation of generations.

In the wingless Orthoptera, the young so closely resemble the perfect insects, that there is nothing which in ordinary language would be called even a metamorphosis.

In those Orthoptera which eventually acquire wings, there is of course a well-marked difference.

In *Chloëon*, though the changes are gradual, the difference between the larva and the imago is very considerable, and we have seen that the action of external forces produces changes which have no reference to the form of the perfect insect.

In caterpillars we have a typical class of metamorphoses.

Until recently, however, we knew of no case in which a larva produced more than one perfect insect*. Insects never multiply by buds, and almost always the external form is acquired before the organs of reproduction are mature. Recently, however, Professor Wagner of Kasan has discovered that the larvæ of certain Cecidomyias have the faculty of producing other larvæ, so that they present a true case of alternation of generations. Thus, then, we see that insects present every gradation, from growth to alternation of gen-

* The instances in which certain insects breed while their wings are but imperfect, might here have been cited. But as there is much difference of opinion among entomologists as to these cases, I have thought it better to take one about which no question is likely to arise.

erations ; we see, from a single fact, how metamorphoses and alternate generations may have originated, and we find reason to suppose that in the course of time the latter phenomenon may become more frequent than it is at present.

It is, moreover, evident that there are in the animal and vegetable kingdoms two kinds of dimorphism. The term has generally been applied to those cases in which—as in the ant and bee in animals, and the Primulas among plants—the perfect individuals are divided into two forms. In fact the sexes themselves constitute a kind of dimorphism. In these cases the forms are not alternate. When, however, external forces act on the young in one manner, and on the mature form in another, they tend to produce different forms, which do not complement, but succeed, one another. I have elsewhere proposed to distinguish this form of dimorphism, under the name of dieidism or polyeidism. In polymorphism the chain of being divides at the extremity ; in polyeidism it consists of dissimilar links.

Finally, the speaker said, "The principal conclusions which I would impress on you this evening are—

"1. That the presence of metamorphoses in insects depends, in great measure at least, upon the early state in which they quit the egg.

"2. That metamorphoses are of two kinds—developmental and adaptational.

"3. That the apparent abruptness of the changes which they undergo arises in great measure from the hardness of their skin, which permits no gradual alteration of form, and which is itself rendered necessary in order to afford sufficient support to the muscles.

"4. That the immobility of the pupa or chrysalis depends on the rapidity of the changes going on in it.

"5. That although the majority of insects go through three well-marked stages after leaving the egg, still a large number arrive at maturity through a somewhat indefinite number of slight changes.

"6. That the form of the larva of each species depends in great measure on the conditions in which it lives.

"When an animal is hatched from the egg in an immature form, the external forces acting upon it are different from those which affect the mature form; and thus changes are produced in the young, bearing reference to its present wants rather than to its ultimate form.

"7. When the external organs arrive at this final form before the organs of reproduction are matured, these changes are known as metamorphoses; when, on the contrary, the organs of reproduction are functionally perfect before the external organs, or when the creature has the power of budding, then the phenomenon is known as alternation of generations.

" Insects present every gradation, from simple growth to alternation of generations.

"8. Thus, then, it appears probable that this remarkable phenomenon may have arisen from the simple circumstance that certain animals leave the egg at a very early stage of development, and that the external forces acting on the young are different from those which affect the mature form.

"9. The dimorphism thus produced differs in many important respects from the dimorphism of the mature form which we find, for instance, in the ants and bees; and it would therefore be convenient to distinguish it by a different name.

"But there is still another aspect under which, if time had permitted, the metamorphoses of insects might have been regarded. In one or two cases, indeed, I have sketched very briefly and imperfectly the habits and mode of life of particular insects. A whole course of lectures might be filled with such life-histories. The various manners in which different insects provide for the wants of their young are most remarkable, and all the more so because their wants are so different from those of the perfect insects themselves.

"Thus the butterfly, which lives on honey, and did live on leaves, lays her eggs on a twig. She seems to feel that honey will not suit her young, and that the leaves will wither and fall before another spring comes round.

"The gnat, which lives in the air and feeds on blood, lays her eggs on the surface of water; and the sugar-loving housefly knows that very different food is necessary for her young.

"The nut-weevil chooses the embryo of the nut; the goat-moth the bark of the willow; the *Rhipiphora* braves the dangers of the wasps' nest; the *Œstrus* lays on cattle; the *Ichneumon* in caterpillars; the gall-fly in the still almost imperceptible bud; and some insects even in the eggs of others.

"Generally the larvæ forage for themselves; but in some cases the mother supplies her young with food. Thus the solitary wasp builds a cell and fills it with other insects. If, however, she imprisoned them while alive, their struggles would infallibly destroy her egg; if she killed them, they would soon decay, and the young larva, when hatched, would find, instead of a store of wholesome food, a mere mass of corruption. To avoid these two evils, the wasp stings her victim in such a manner as to pierce the centre of the nervous system, and the poison has the quality of paralyzing the victim without killing it. Thus deprived of all power of movement, but still alive, it remains some weeks motionless and yet fresh.

"But, perhaps, the ants are the most remarkable of all. They tend their young, they build houses, they make wars, they keep slaves, they have domestic animals; and it is even said that in some cases they cultivate the ground.

"Nor must it be supposed that even now the habits of insects are anything like thoroughly known to us. In spite of Réaumur and De Geer, the two Hubers, and many other excellent observers, there is in this subject still a wide field for patient and conscientious labour; the observations already made have been far from exhausting the mine, though amply sufficient to prove the richness of the ore."

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