III. *On the Development of* Chloëon (Ephemera) dimidiatum.—Part I.

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(Plates XVII. & XVIII.)

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Introductory Remarks.

BURMEISTER expresses, I believe, the opinion general among entomologists when he says that, excepting a few very rare anomalies, "we may observe four distinct periods of existence in every insect, namely, those of the egg, the larva, the pupa, and the imago" *. In most cases (as, for instance, in Diptera, Lepidoptera, Hymenoptera, and Coleoptera), the larva is said to be a fleshy maggot or caterpillar, quite unlike the imago; and these insects are therefore called by Prof. Westwood "Heteromorpha." In the Orthoptera, Hemiptera, Euplexoptera, and many Neuroptera, on the contrary, the larvæ much more closely resemble the imago; and these groups are therefore called by Prof. Westwood "Homomorphous" insects. In them, the pupa is said to differ from the larva in possessing wing-rudiments on the back of the two posterior thoracic segments.

These differences, however, relate only to what we see in insects after birth; while, if we are to treat the question in a philosophical manner, we must examine the development as a whole, from the commencement of the changes in the egg, up to the final completion of the animal, and not suffer ourselves to be misled by the circumstance that insects do not all leave the egg in the same stage of embryonal development. Quatrefages has well said, "La larve n'est qu'un embryon à vie indépendante" †, expressing with his usual brilliancy the idea which we owe, I believe, to Prof. Owen‡, who says, "The insects which are said to be subject to the semicomplete and incomplete metamorphosis pass through the same kind and amount of change as those characterized by the obtected or coarctate pupa. The differences resolve themselves essentially into the place where, and the time in which, they assume and quit the vermiform state." And again, "The Orthopterous and Hemipterous insects, characterized in entomology by a semicomplete metamorphosis, are, at one stage of their development, apodal and acephalous larvæ, like the maggot of the fly; but, instead of quitting the egg in this stage, they are quickly transformed into another, in which the head and rudimental thoracic feet are developed to the degree which characterizes the hexapod larvæ of the *Carabi* and *Petalocera*." I know not upon what authority this broad statement rests. Mr. Murray, indeed, at one time supposed that in some eggs of *Blatta* he had seen the larva in this grub state, but this statement has since been abandoned by its candid and

* 'Manual,' translated by Shuckard, p. 30. See also Curtis in the Journ. Agricult. Soc. vol. ii. p. 192.

† Métamorphoses de l'Homme et des Animaux, p. 133.

‡ Lectures on the Comparative Anatomy, &c., of the Invertebrate Animals, 2nd edit., pp. 423, 424.

ingenuous author. With the exception of this genus, I am not aware that the development of any Orthopterous or Hemipterous insect has been worked out.

Two memoirs bearing on the subject have, however, since appeared, namely, Zaddach's "Die Entwickelung des Phryganiden-eies," and Huxley's memoir on *Aphis*, which appeared in the Transactions of this Society. Zaddach figures (fig. 19) and describes a state in which the embryo of *Phryganea* is a grub, with an imperfect, though segmented, body, but without any appendages; yet, he says, this condition lasts only for a short time, and may therefore easily be overlooked. Prof. Huxley also* has shown that there is, in the development of *Aphis*, a particular period at which the embryo presents, on the sternal side, traces of segmental divisions, without having even rudiments of legs. Thus then it appears that in both these cases the so-called "larva" is preceded by an apodal body, corresponding in some respects with the grubs of Diptera. It is unnecessary to remark, that the change from this grub-like embryo to the so-called "larva" is produced by gradual modification, and not by any process of moulting. But, in considering the matter, we must also bear in mind that the apodal body of the embryonic *Aphis* or *Phryganea* is in a very different condition from the maggot of a fly. Not only are the internal organs, so far as our information goes, entirely undifferentiated, but the dorsal walls themselves are not as yet formed.

But however this may be, and even in the case of insects with an incomplete metamorphosis, it is the general opinion of entomologists that the life may be divided into three periods, each marked by a change of skin and an alteration of form. "After the first change," says Burmeister†, "the larva has merely increased in size; but during this second period of its existence, the rudiments of the wings form beneath the skin; consequently, after the second moulting, these incipient wings present themselves externally as small leaves, which cover the sides of the first abdominal segment: these larvæ are called nymphs, being analogous to the pupa-state of other insects. When this pupa again moults, the insect attains its perfect condition."

Prof. Owen also, although, as we have seen, he considers that the period corresponding to the larva of Diptera, Lepidoptera, &c., is, in insects with an incomplete metamorphosis, passed in the egg, still appears to consider that the life even of these last falls into three well-marked periods.

I shall, however, show that in several insects there is no such well-marked, threefold division; and that, in the Ephemeridæ at least, the young insect gradually attains its perfect condition through a series of more than twenty moultings, each accompanied by a slight change of form. Fig. 10 represents the state at which the first rudiments, or rather indications, of wings make their appearance, in the form of a scarcely perceptible production of the posterior meso- and metathoracic angles; and it will at once be perceived that the amount of change is very slight indeed.

Probably our opinion has been too much influenced by the well-known metamorphoses of Lepidoptera, and we have expected to find the same changes and the same uniformity throughout the insect-world.

Even now, however, a certain number of exceptional cases are upon record, and we

* "On the Organic Reproduction and Morphology of *Aphis*," Linn. Trans. vol. xxi. part 3. † *Loc. cit.* p. 429.

shall probably find that there are far more variations than we are most of us, at present, prepared to accept.

Among Coleoptera, we owe principally to Newport and Fabre a knowledge of the curious and complicated metamorphoses through which *Meloë* and *Sitaris* arrive at maturity.

Among the Diptera, the interesting case of the "Pupipara" has long been known; and I have also shown * that the curious larva of Lonchoptera turns into a simple grub inside the cast skin, before it developes the rudimentary, or at least imperfect, organs which are characteristic of the pupa.

The metamorphoses of the Physapoda (*Thrips*) are thus described by Mr. Haliday † :— "Metamorphosis incompleta, per duas ætates intermedias progrediens, scilicet, propupa et pupa, asitophaga, tardigrada. Larva oculorum lenticulis paucis dissitis."

M. Yersin has described several stages in the development of *Gryllus campestris*.

Among the Homoptera, I have satisfied myself that in *Typhlocyba*, a genus of Cercopidæ, there are at least five well-defined stages, while in *Aphis* also there are more than three.

Among the Neuroptera also, the genus *Psocus* seems to pass through at least four conditions.

No doubt this list might easily be augmented; but it is at least sufficient to show that the presence of three stages, and three stages only, is far from being so generally true of insects as has been supposed.

If now we attempt to ascertain the secondary laws which regulate the form under which any given family of insects is hatched, we shall find that, the whole development being in a certain sense in all cases the same, the rapidity with which the different organs are developed varies in different insects; and that the condition at birth depends partly on the group to which it belongs, but perhaps still more on the manner in which it is to live.

Thus, those larvæ which are internal parasites, whether in animals or plants, belong to the vermiform state; and the same is the case with those which are intended to live in cells, and to depend on their parents for food. On the other hand, larvæ which are to burrow in wood have strong jaws, and somewhat weak thoracic legs; those which are to feed on leaves have the thoracic legs more developed.

Now the Hymenoptera, as a general rule, belong to the first category: the larvæ of the Ichneumons, &c., which live in animals,—those of the Cynipidæ, which inhabit galls,—and those of Ants, Bees, Wasps, &c., which are fed by their parents, are all fleshy, apodal grubs. On the other hand, the larvæ of *Sirex*, which are wood-burrowers, quit the type which is common to the majority of the order, and remain in the egg until they have developed small thoracic legs. Again, the larvæ of the Tenthredinidæ, which feed upon leaves, closely resemble the caterpillars of Lepidoptera, even to the presence of abdominal prolegs. There is, however, some little variety in this respect, some species having eleven pairs, some ten, some nine, while the genus *Lyda* has only the three thoracic pairs.

Perhaps, however, the most remarkable cases of all are the genera *Meloë* and *Sitaris* among the Coleoptera. The insects of this group are at first active hexapod larvæ; but

* Entomological Transactions, 1862. † British Museum Catalogue of Homopterous Insects, p. 1094.

having introduced themselves into the cells of certain species of Hymenoptera, they undergo a retrograde metamorphosis, lose their legs, and emerge as grubs, not altogether unlike those whose places they have usurped.

When an insect is destined throughout life to exist in the same manner and to use the same food, then it leaves the egg with the principal organs constituted in the same manner as in the imago.

Thus, then, we may lay it down as a general rule, that the form of an insect at its birth is a function of the life which it is to lead, and of the group to which it belongs; and that insects are generally born at a period in their development as early as is consistent with the life to which they are destined.

There are doubtless many apparent exceptions. Thus, among the Diptera, lignivorous larvæ, like those of some Tipulidæ, terricolous larvæ, like those of others, and predaceous larvæ, as in *Syrphus*, are all fleshy, apodal grubs. A better acquaintance with their habits would probably explain the anomaly: the lignivorous Tipulidæ, for instance, principally affect decaying wood; and in the case of *Syrphus*, we may already see that the condition of the young larva, surrounded by crowds of helpless Aphides, differs in reality but little from that of an internal parasite.

But while the preceding has reference to the degree of change which takes place after birth, the manner also must be considered. In some insects the development is slow and gradual, while in others the growth is effected without any material change of form, and the metamorphosis, if not sudden, is at least comparatively rapid.

Now, as long as any organ continues to be in a state of functional activity, the changes taking place in it must be slow and gradual; when therefore the metamorphoses are rapid, and are accompanied by only one or two changes of skin, we at once see that they necessitate a period of quiescence. When, moreover, as in the Lepidoptera, a mouth, originally mandibulate, is destined to become suctorial, any such gradual change would be inconvenient or impossible; the insect might starve in the meantime. Here, therefore, it becomes desirable that the change should be rapid. The Hemiptera, indeed, which are suctorial, are also active through life; but in them the mouth of the larva is constituted in the same manner as that of the imago.

Again, when extensive changes have to take place in the muscular system, a period of enforced quiescence is the result. Some of the aquatic Diptera offer, indeed, an apparent exception; but in these the muscles which move the pupa are those of the abdomen, while those of the imago are situated in the thorax.

It may still be asked, to what general cause can we ascribe these metamorphoses? why should not insects remain in the egg until their generic and specific characters are fully developed? Omitting for the present all consideration of terrestrial animals, we cannot but be struck by the poverty of the freshwater fauna when compared with that of the ocean. The Mollusca are far less numerous and less varied; of the Fish the same may be said; compared with those of the sea, our freshwater Bryozoa are quite insignificant in numbers; the Hydrozoa are represented by only two genera. Among Crustacea, the Podophthalms have in this country but one freshwater species, the Isopods one, the Amphipods very few; Entomostraca, indeed, are well represented, but Cirrhipedes are

altogether absent; neither the Actinozoa nor the Echinodermata have a single freshwater representative.

But while so many families are absent, their places are not left unoccupied. Not only do the insects themselves in a great measure restore the balance, but their larvæ also do much to relieve the monotony. Many situations are thus filled; much food is thus perhaps made available which would not otherwise contribute towards the support of animal life.

Insects, indeed, are not the only animals which undergo metamorphoses even after birth; every subkingdom supplies some instance. In this manner perhaps the world supports more life, and the sum of happiness is therefore greater, than would be the case if every creature arrived at its perfect form before quitting the egg.

I have still used the old word "larva" to denote the first part of the life of an insect after birth. If, however, there is any truth in the preceding observations, it is evident that the so-called "larva" of a Fly corresponds properly neither with that of a Moth nor with that of a Grasshopper, and it is always inconvenient to use one word with several meanings. Much of the confusion in political economy has arisen from the unfortunate use of the word "money" to mean either capital in general or the circulating medium in particular.

And yet it would be very difficult to remedy the inconvenience in the case of the word "larva." Not only is it almost necessary for entomology that there should be one word to denote the early stages in the life of an insect, but it would be perhaps impossible to give the word a more definite meaning without restraining it within very narrow limits. In fact, insects leave the egg in every possible stage of development. The maggots of Flies, in which the appendages of the head are rudimentary, belong to a lower grade than the grubs of Bees, &c., which have antennæ, mandibles, and maxillæ, labrum, labium, and, in fact, all the mouth-parts of a perfect insect.

The caterpillars of Lepidoptera are generally mentioned with the larvæ of Diptera and Hymenoptera, and placed in opposition to those of Orthoptera, Hemiptera, &c. But, in truth, the possession of thoracic legs places them, as well as the similar larvæ of the Tenthredinidæ, on a decidedly higher level, while in the development of the cephalic appendages there is, as already mentioned, a marked difference between the maggots of Flies and the grubs of Bees.

Thus then the period of growth (that in which the animal eats, and increases in size) occupies sometimes one stage in the development, sometimes another; sometimes, as for instance in the case of *Chloëon*, now to be described, it continues through more than one,—or, in other words, growth is accompanied by development.

But, in fact, the question is even more complicated than this. It is not only that the larvæ of insects at their birth offer the most various grades of development, from the grub of a Fly to the young of a Grasshopper or a Cricket; we have not to deal only with a simple case of gradation, but we have a series of gradations, which would be different according to the organ which we took as our test. We have already seen that the larvæ of *Phryganea* and those of Diptera and Hymenoptera differ in the development of the viscera and of the appendages,—the viscera being in the two latter orders formed before

the appendages, while in *Phryganea* and some other insects the reverse appears to be the case; and we shall even find in the same species minor variations in the relative development of different organs.

The Development of Chloëon.

With these few introductory observations, I will pass on to consider the development of the larvæ of *Chloëon dimidiatum**, which are very common in our Kentish ponds.

They have not escaped the notice of previous observers, but I am not aware that either they or any other insects belonging to the homomorphous series have ever been watched through their various changes. The development of the Ephemeridæ is thus described by Pictet† :—"Les métamorphoses sont incomplètes. Les larves vivent dans l'eau, s'abritant dans la vase ou sous les pierres. Elles rappellent plus ou moins la forme de l'insecte parfait, sauf qu'elles manquent d'ailes, qu'elles sont plus fortes, que leur bouche est mieux armée, qu'elles ont toutes trois soies caudales, et que leur abdomen est muni sur ses côtés d'organes respiratoires externes de forme variable. La nymphe, agile comme la larve, n'en diffère que parce qu'elle porte des rudiments d'ailes." Prof. Westwood, again, says that the larvæ differ from the pupæ "only in the absence of rudimental wing-covers;" and other naturalists have, I believe, but repeated this statement.

First State (Pl. XVII. fig. 1).

The smallest specimens which I have seen were only $\frac{18}{800}$ths of an inch in length, quite colourless and transparent. Not having hitherto had an opportunity of breeding the insect from the egg, I am of course unable to state whether this is really the condition in which the young *Chloëon* leaves the egg; but for the present I shall, for convenience, assume that it is so. The head is shaped somewhat like a capital ⍓, and is $\frac{3}{800}$ths in width. The eyes are five in number, round, and equal in size. Two are situated on the posterior angles of the head; two are in front, and somewhat further apart, so that, being placed on the sloping side of the head, they look elliptic, though in reality round. The fifth, which perhaps is normally composed of two, lies more in front and in the middle line. The general appearance of all five is similar; and I could see no trace of any facets.

The antennæ (fig. 18) are $\frac{11}{800}$ths in length, and consist of thirteen segments. The first is short, and tapers from the base to the apex; the second is also short, but tapers in the opposite direction, *i. e.* from the apex to the base. The third segment is long and cylindrical; it has two or three hairs near the apex. The four following segments are together about equal in length to the third; the divisions between them are, however, but slightly marked, and the seventh only has the usual hairs at the apex; so that it may be doubted whether it would not be perhaps more correct to consider this division of the antenna as constituting only a single segment. The same description applies to the four following segments; the twelfth tapers to the apex, and bears a fine, needle-like body, which might be called a seta almost as well as a segment.

* The name has been kindly determined for me by my friend Mr. F. Walker.

† Histoire naturelle des Névroptères: Ephémérines, p. 5.

The separations between the three thoracic segments are not very distinct. The prothorax is rather the largest of the three, and, as does also the metathorax, equals the head in breadth.

The legs are well developed, and are adapted for walking, but not for swimming; still they are not strong enough to support the body out of water. They consist of the usual five divisions: the two basal are short, and might almost be considered as one; the other three are long and cylindrical, the femur being the longest, and the tibia rather shorter than the other two.

The claw is large, and resembles a clasp-knife in shape. There are a few strong simple hairs scattered over the legs, two or three at the apex of each segment, in addition to which the tarsus has one near the middle. Those which are on the upper side of the leg are delicate and thin; but those on the under side are much stronger, as the insect rests on them when walking. The tarsus has only one of these supporting hairs.

The abdomen consists of ten segments, which decrease gradually in breadth from the first to the last. The eighth, ninth, and tenth are rather longer than the rest. The second and four following segments increase slightly from in front to behind: this condition is no doubt connected with the subsequent production of the so-called gills; it is most strongly marked in the third, fourth, and fifth segments, just as the gills attached to these segments will at first be the largest.

No tracheæ are as yet visible; respiration must therefore take place by the outer surface of the body.

The posterior segment bears two long, many-jointed caudal filaments or tails. They are rather longer than the body, though very slightly so, and consist of nineteen segments. The basal is $\frac{5}{8\,0\,0}$ths in length, cylindrical, slightly enlarged on the inner side near the base, and has several transverse ridges, which have at first sight much the appearance of joints, but which are in reality rather comparable to those numerous minutely toothed ridges, which, when the insect is rather older, give the whole skin a shagreened appearance. The apex is surrounded by a circle of strong teeth, near which, or rather closer to the terminal ridge, are one or two minute hairs.

The second division of the tail is $\frac{4}{8\,0\,0}$ths in length; it is divided into five segments by ridges which, though resembling those above described, are (and especially the apical one) more strongly marked and more persistent. As in the basal segment, the terminal ridge bears three or four hairs, and the apex of the division is surrounded by a circle of short spines.

The third division of the organ is likewise divided by ridges into five segments, which, except that they are slightly slenderer, in all respects resemble those of the second division.

The six following segments call for no special description. The twelfth, thirteenth, fifteenth, sixteenth, and seventeenth are of moderate length, the fourteenth being shorter. The sixteenth and seventeenth segments have each a hair near the apex. The eighteenth is longer and slenderer; the nineteenth, like the terminal segment of the antennæ, tapers to a very sharp point, and resembles a hair almost as much as a segment.

These appendages do not appear to be as yet of much use in swimming, which is, I think, at this age effected principally by means of the abdomen. This latter is very moveable,

and is continually jerked upwards, even so much as to throw the caudal setæ in front of the head, which gives the young insects a singular resemblance to the caterpillars of the Puss-moths. I have especially noticed that this movement takes place when any still minuter creature touches the young *Chloëon*; the tails, therefore, most likely serve as organs of defence, but perhaps also partly for sensation. The larger larvæ never bring them forward over the body, perhaps because the continual vibration of the branchiæ renders such a movement unnecessary.

In moulting the insect does not split the skin of the thorax, as is so generally the case, but merely that on the upper part of the head. It is wonderful, indeed, how it can escape through so small an orifice.

Second State (fig. 2).

A specimen, which I met with in the above-described condition on the 21st September, had undergone a moult by the following morning. From the analogy of subsequent development, it is most probable that the first state lasts only two or three days at most. In the second state the total length is still only $\frac{20}{800}$ths. The general form of the body is the same as before; but the posterior angles of the second and four following segments are, especially those of the third, fourth, fifth, and sixth, more strongly produced.

The antennæ (fig. 19) are $\frac{15}{800}$ths in length, but they consist of only the same number of segments as before. The first two and the last ten, moreover, have scarcely increased in size; but the third, which in the first stage was only $\frac{5}{1600}$ths in length, has about doubled itself. We shall presently see how great a part this segment takes in the subsequent development of the organ.

The tarsi have two "supporting" hairs.

The two tails have increased to a length of $\frac{25}{800}$ths, and consist of twenty segments. Here again, as in the antennæ, almost the whole change has taken place in one segment, which, however, is in the present case the basal one. The remainder are almost exactly as they were before. As already mentioned, the basal segment was in the first stage $\frac{5}{800}$ths in length; in the present it has divided into two segments, which, taken together, are $\frac{9}{800}$ths; and we see therefore that almost the whole increase of length is in this one part. The second segment is somewhat shorter than the first. The minute ridges surrounding the basal segment have almost disappeared.

Between the two tails is a minute knob, which, as we shall see, is destined to become far more important than its present appearance would indicate.

The whole skin of the insect, including not only that of the body, but also the antennæ, legs, and caudal appendages, is beset with little teeth, which fall more or less into regular rows. The last row on each segment consists of teeth much larger than the others, and forms a sort of fringe of spines. This applies not only to the body, but also to the legs and basal part of the antennæ and tail. On the segments of the body, these spines are most distinct on the central part of the dorsal margin, and especially on the posterior segment, where also two or three of the spines are much larger than the rest.

On the sides of the body are several small circles, which look almost like holes, but of which I cannot explain the function. In very young larvæ they are few in

number, but in the later stages they become very numerous. A specimen which I found on the 21st of September, and which then resembled fig. 1, changed its skin on the following morning, and then remained without much alteration until the 25th, by which time it had grown to $\frac{22}{800}$ths, when it moulted once more, and so entered the

Third State (fig. 3),

which lasts for two or three days, during which the insect grows from $\frac{22}{800}$ths to $\frac{26}{800}$ths or $\frac{28}{800}$ths in length.

The posterior eyes are now about twice as large as the three front ones; so that the distinction between eyes and ocelli begins at this early stage, though we have seen that at first they are very similar. I could not distinguish any facets.

The antennæ (fig. 20) are $\frac{20}{800}$ths in length, and now consist of fifteen segments, the two new ones being formed at the expense of the third, in which also almost the whole increase of length has taken place. The apices also of these three segments differ from those of all the others in being surrounded by a circle of teeth, as was, indeed, the case with the third segment in the preceding state, when, however, the teeth were smaller and less conspicuous. Of the two new segments, the basal one is rather the shorter. The terminal segments have increased slightly in size, but not in number; indeed, several of them are even less strongly marked than before; this is particularly the case with the two which are now the tenth and eleventh, and between which scarcely any division is visible.

The tarsi have three supporting hairs.

The posterior angles of the second and four following abdominal segments are much less produced than before; but then, on the other hand, each of them supports a small, oval, leaf-like appendage, the first appearance of the branchiæ. Those attached to the third and fourth segments are the largest, and are almost as long as the segments themselves; the second and fourth are somewhat smaller; the fifth still less; while the first is almost rudimentary. The seventh segment has the posterior angles somewhat produced, in preparation for the posterior branchiæ, which will make their appearance after the next moult. I could see no tracheæ either in the body or in the gills, even in this, the third stage in the animal's free existence.

The two tails are now $\frac{34}{800}$ths in length, and consist of twenty-four segments,—the whole increase in the number of joints, and almost all that in the length, being due to the basal portion, which is almost double as long as it was before, and constitutes now just half of the total length. I believe that what was in the last stage the second segment now forms the fifth and sixth, the four basal being due to the subdivision of the first. Each of these segments has a ring of teeth round the apex; but the rings are not all equally well marked, those round the second, fourth, and sixth being larger than the other three. Each of the six basal segments has also one or two hairs near the apex. The eighteen terminal segments are almost unaltered.

The little knob between the two tails is larger than before, and pyriform.

Fourth State (fig. 4).

The fourth state, like the third, lasts only two or three days, at the end of which time the insect has attained a length of about $\frac{32}{800}$ths.

The antennæ (fig. 21) are $\frac{24}{800}$ths in length, and the segments are seventeen in number, the increase both in length and number being again due to the third segment, the rest of the organ having remained almost stationary.

Owing to the fact that the split, through which the insect emerges, runs along the top of the head, it is difficult to study the development of the eyes; but I noticed that on each side of the upper part of the head there was a group of the curious "rings" which I have already mentioned.

The tarsi still have three or four supporting hairs, the number being the same on all the legs.

The gills are more developed than before; the five intermediate pairs stand out at right angles with the body, while the first and last are still rudimentary, the first, however, being the more advanced of the two. The five intermediate gills begin to vibrate soon after the change of skin, but the motion is not so continuous as it subsequently becomes. The tracheæ in them, though small, are easily visible, and communicate with the great longitudinal trunks. The circulation of the blood is also apparent, and the beating of the heart can be distinctly seen. In form the gills resemble a sharp pear; they are about $\frac{1}{400}$th in length; the front margin is, for half its length, strengthened by having the border somewhat thickened; the margin is more or less waved; and each gill, excepting the first and last, which are still rudimentary, has a small hair in the middle of the free edge, as well as sometimes one or two elsewhere.

The caudal appendages are about $\frac{35}{800}$ths in length, with twenty-eight segments.

The basal part now consists of ten segments, instead of six: my impression is that the four basal have divided.

The terminal segments are almost unaltered. The circles of spines are largest round the second, fourth, sixth, and eighth segments. In addition to the two or three hairs near the apex of each segment, the ninth has on the inner side, somewhat nearer to the apex than the base, a long hair, which is the commencement of the swimming-fringe.

The knob between the two tails is again larger, but still consists of only one segment.

Fifth State (fig. 5).

The fifth state, like the third and fourth, lasts for two or three days, beginning when the insect is about $\frac{32}{800}$ths in length.

The antennæ are $\frac{25}{800}$ths to $\frac{32}{800}$ths in length, and consist of twenty segments. The ten apical ones are almost unaltered: the arrangement of the hairs is as before, and, what is very remarkable, these segments have scarcely increased at all in size; indeed, their length is little greater than in the smallest specimen examined. Some, however, of the segments are much less strongly marked, and, indeed, but for their homologies with the same parts in earlier stages, I should have considered that there were only five segments in this portion, as practically the first four on the one hand and the second three on the other have coalesced.

I did not, in this state, see any facets to the eyes; but the posterior pair differ from the anterior three not only in size but in appearance, the posterior ones being brown, with indistinct traces of the separate eyes,—the ocelli, on the contrary, being composed of a greyish mass set in a black substance.

The supporting hairs on the tarsi are five or six in number.

The anterior gills have increased in size more than the others, and are now larger than the sixth pair. The posterior ones are still rudimentary. The first pair now commence to vibrate, but less continuously than the others, being often quiet when the five following pairs are in motion. The posterior gills differ from all the rest in possessing no power of vibration, either at this age or at any subsequent period.

The caudal appendages are $\frac{44}{800}$ths in length. The eighteen terminal segments are unaltered, except that the first five of them have coalesced, so that they can no longer be distinguished as separate segments. The basal portion now consists of seventeen segments; so that there are thirty-five altogether. As before, the circle of spines is larger round the second, fourth, sixth, and eighth than on the other segments. The swimming-fringe commences on the eleventh segment, and is represented by a single hair on the inner side, and somewhat nearer the apex than the base. Some of the segments, however, have two such hairs.

The central caudal appendage is again about twice as long as before, and almost equals the basal segment of the lateral tails. It is, however, still unjointed.

Sixth State (fig. 6).

The animal moults again when it has attained the length of from $\frac{35}{800}$ths to $\frac{40}{800}$ths.

The antennæ have a length of $\frac{35}{800}$ths, and the third segment has again divided into three parts, of which the basal is the longest and the middle the shortest; so that, from the fourth to the twelfth inclusive, the segments increase in length as they diminish in diameter. If no other change had taken place, the total number of segments would, of course, under these circumstances, be twenty-two; but, practically, there are only eighteen, those four segments which were originally the fourth, fifth, sixth, and seventh having completely coalesced, and the same thing having taken place also with the two following.

The large posterior eyes now consist of a number of dark spots on a paler ground.

The tarsi have seven supporting hairs.

The lateral tails are $\frac{50}{800}$ths in length, and consist of twenty-six segments. The three terminal segments have undergone little alteration, the two basal divisions of five segments and the four basal segments of the third quintet (if I may use the expression) having respectively coalesced, so as to form now only four segments. This terminal portion of the tail, therefore, resembles the terminal part of the antennæ in the gradual coalescence of originally distinct segments, and offers an additional resemblance in the remarkable fact that it has not at all increased in length. The basal segment, on the contrary, like the third segment of the antennæ, has rapidly developed itself. When the whole organ was $\frac{21}{800}$ths in length, it measured $\frac{5}{800}$ths; in this sixth state it has produced, directly or indirectly, nineteen new segments, which have a length of $\frac{34}{800}$ths, and have therefore almost monopolized the whole increase.

In the antennæ, however, the new segments appeared to me to be always detached from the apical extremity of the third segment itself; in the tails, on the contrary, the young segments again subdivided,—a difference connected perhaps with the much more rapid increase of length. Only a few, however, subdivide at each moult: thus, the number, which in the last stage was seventeen, is now twenty; the consequences are that the length of these segments does not increase so regularly as is the case with the growing part of the antennæ, and that the circles of spines round the apices are of different sizes, being of unequal age. The two basal segments appear generally to divide, so that the spines at the apices of the second and fourth segments are larger than those on the first and third. In some specimens, however, the two tails differ slightly in this respect. The fringe now commences on the eighth segment, which, with the three following, has a single hair on the inner side; the next two or three have each two hairs, then follow two or three with three, after which they again decrease. They are confined to the developing part of the tail, and are independent of, and in addition to, the ordinary apical setæ.

The central tail is now $\frac{4}{800}$ths in length, and consists of two or three, but indistinctly separated, segments. It is stout in proportion to its length, and terminates in a rounded, soft extremity, very much as the lateral tails do if by any accident they have been injured. This mode of termination is not, however, in the present case the result of injury, but is probably connected with the rapid growth which is taking place.

Seventh State (fig. 7).

The sixth state does not last much longer than the earlier ones. In my specimens, the next moult took place when the insects were from $\frac{38}{800}$ths to $\frac{40}{800}$ths in length.

The antennæ are about $\frac{36}{800}$ths, and consist of twenty segments, the third having again divided into three.

The supporting spines on the tarsi have again increased in number.

Up to this time the branchiæ have been single, and, indeed, they are so still; but the larger ones already show on the posterior margin a slight lobe, which eventually becomes a second plate (Pl. XVIII. fig. 22).

The lateral tails are slightly longer than the body, and consist of thirty-two segments. The hairs forming the commencement of the fringe are rather more numerous. The terminal portion of the tail is unaltered.

The middle tail is from $\frac{8}{800}$ths to $\frac{12}{800}$ths in length, and consists of about six segments, one or two of which, however, are sometimes very indistinct.

Eighth State (fig. 8).

The insect moults again in about three days, when it has a length of from $\frac{45}{800}$ths to $\frac{50}{800}$ths.

In a specimen $\frac{55}{800}$ths in length, the antennæ were $\frac{46}{800}$ths in length. They consist of twenty-three segments, the third having divided into four; the penultimate segment has been becoming a little shorter at each moult.

The secondary lobe of the branchiæ is larger and more distinct.

The lateral tails are about $\frac{60}{800}$ths in length, and consist of about thirty-six segments. The circles of spines are most strongly marked on the second, third, fifth, seventh, ninth, eleventh, and thirteenth segments. The fourteenth and five following segments are slightly darker than the rest. The fringe begins on the ninth segment, and extends to the twenty-sixth, inclusive. None of the segments have as yet more than four setæ.

The middle tail has increased to $\frac{25}{800}$ths, and possesses twelve segments. At its base it is almost as broad as the lateral ones. As in them, the apex of each segment is surrounded by a circle of small spines, and has two or three small hairs, in addition to which the tenth and eleventh have on each side, near the apex, a longer hair. These are the commencement of the swimming-fringe. The skin of the central tail has the usual shagreened appearance.

Ninth State (fig. 9).

While large specimens are often as much as $\frac{50}{800}$ths when they enter the eighth stage, small ones, even in the present condition, are only $\frac{48}{800}$ths in length. This, together with the fact that out of the specimens which I examined not one in twenty had escaped some injury to the tails or antennæ, rendered a precise determination of the exact length and number of segments in each appendage very difficult and very slow *.

I do not indeed suppose that mutilation is so frequent while the insects are in their native ponds, but the process of capture must necessarily be very injurious to such delicate little creatures.

A specimen $\frac{60}{800}$ths in length had antennæ of almost exactly the same length, and lateral tails $\frac{68}{800}$ths in length.

The antennæ consist of about twenty-six segments, the third having again divided into four. I say, however, about twenty-six, because the upper part of the third segment shows indications of another joint, which will become distinct at the next moult, and which some naturalists might even consider so now.

Up to this time no traces of wings have been present. Now, however, the posterior dorsal angles of the meso- and metathorax are slightly produced, so slightly, however, that it is indeed scarcely perceptible. The mesothorax is a little larger than the metathorax, but in form they are almost exactly similar.

The apical circles of spines on the lateral tails are most strongly marked on the second, third, fifth, seventh, and eleventh segments. On some of the segments the fringe is represented by five setæ.

The central tail is about $\frac{32}{800}$ths in length, and consists of eighteen segments. The fringe is appearing on the twelfth and five following segments. The circles of spines are most strongly marked on the second, fourth, sixth, and tenth segments.

* As the insects grow older, these mutilations become more deceptive. It is always easy to distinguish them at first; but when after several moults the injury is almost repaired, individuals thus altered may easily be taken for normal specimens.

Tenth State (Pl. XVIII. fig. 10).

In the ninth stage the insect adds about $\frac{1}{100}$th of an inch to its length; as, however, they are not all of equal size when they enter it, so also at the next moult they vary from $\frac{55}{800}$ths to $\frac{75}{800}$ths.

A specimen $\frac{55}{800}$ths in length had antennæ $\frac{58}{800}$ths in length. They consisted of twenty-nine segments; but the penultimate has almost disappeared; and the apical would, I think, certainly be considered as a mere seta by any one who saw it in its present condition for the first time.

The posterior angles of the mesothorax are more produced: in the last stage the two posterior thoracic segments were similar, but already the difference between them is well marked.

The central tail is $\frac{40}{800}$ths in length, and is composed of about twenty-four segments. The fringe commences on about the ninth segment, and in some of the segments nearer to the apex it consists of four hairs on each side.

The circles are most conspicuous round the third, fifth, seventh, eleventh, and fifteenth segments. Thus there are now two groups, each consisting of four segments.

On the lateral tails the fringe extends to the thirty-first segment. The apices most strongly marked are the second, third, fifth, seventh, eleventh, and fifteenth. Comparing this with the same organ in the preceding state, it appears that the four segments which were then the eighth to the eleventh are now the twelfth to the fifteenth; that, on the other hand, the sixth and seventh have each divided, and, thus forming the quadruple group from the eighth to the eleventh, have added two segments to the whole organ; the other two new ones having originated in the division of the first and third. In some specimens the apices of the seventh, eleventh, and fifteenth, with the whole of the four following segments, are slightly darkened, a character which is much more strongly marked in some specimens than in others. Some, indeed, have scarcely a trace of it.

The larger branchiæ are now about $\frac{6}{800}$ths in length, and near the middle are almost as broad. Figs. 22, 23, & 24 give an idea of the distribution of the air-vessels in them; the details, however, vary a good deal, even in the two branchiæ forming a single pair, the most usual differences being in the magnitude of the branches *a* and *b*, which are often so large that the main trunk appears to divide into four subequal divisions. The main trunks, as well as the two great longitudinal vessels in the body, are surrounded by a variable deposit of brownish pigment.

Near the base are scattered a few markings, consisting of double circles, which, in subsequent stages, become much more numerous. They resemble those which occur in the skin of the body.

The little lobe already mentioned has become quite distinct. It is more or less reniform, and as yet only $\frac{2}{800}$ths in length. The first and last pairs of branchiæ, however, which have throughout been less advanced than the middle ones, are still single.

A specimen which I isolated on the 8th of September, while it was in the third state, and the account of whose subsequent development, confirmed and checked by comparison with others, has been given above, arrived at the tenth stage on the 27th of September, being then $\frac{65}{800}$ths in length.

Eleventh State (fig. 11).

This specimen moulted again, and so entered the eleventh stage, on the 30th of September, when it measured $\frac{75}{800}$ths in length; sometimes, however, the insect attains a length of $\frac{80}{800}$ths before it moults again.

The posterior angles of the mesothorax cover rather more of the metathorax, the angles of which also are a little more prominent than before.

In a cast skin, which was $\frac{85}{800}$ths in length, the central tail was $\frac{65}{800}$ths, and consisted of thirty-seven segments, without, however, being quite perfect. The circles of spines were, as before, most conspicuous round the third, fifth, seventh, eleventh, and fifteenth, to which was now added the nineteenth segment; here again, therefore, the sixth and seventh had divided into two, while the other two new segments at the base had been produced by the first and third.

Compared with the description given of a specimen in the preceding state, this still leaves three segments unaccounted for; the above specimen was, however, imperfect.

The sixth and seventh segments already show indications of a division—so much so, indeed, that I have some doubt whether they should not be counted as four.

The darkened part extends from the nineteenth to the twenty-fourth segment. The fringe extends to the thirty-second.

In the lateral tails the fringe extends to the thirty-sixth segment, beyond which are nine more, though the organ is evidently imperfect. The principal circles are now the third, fifth, seventh, eleventh, fifteenth, nineteenth, and twenty-third. The twenty-fourth and three following segments are darkened.

Here again, therefore, the plan of development is evidently the same as before.

This stage lasts for about a week, and the insect increases to about $\frac{95}{800}$ths in length. Some specimens, however, like the above, moult again, and so enter the twelfth stage, when they are no more than $\frac{85}{800}$ths.

Twelfth State (fig. 12).

At the next change of skin there is even less alteration in form than has been, up to this time, usual. One of my specimens, which moulted on the 3rd of November, seemed to have the wing-rudiments almost exactly of the same length as before.

The fringe on the lateral tails extends to the thirty-eighth, and that on the central one to the thirty-fourth segment; but they are otherwise without alteration.

In this stage the insect attains a length of about $\frac{90}{800}$ths to $\frac{100}{800}$ths.

Thirteenth State (fig. 13).

In this state the posterior angles of the mesothorax, or, as they may now be fairly called, the rudimentary wings, cover three-quarters of the metathorax, while the posterior angles of the latter segment have undergone little alteration.

The number of new segments added to the antennæ at each moult is larger than at first; and as the growth of the third segment has not increased proportionately in rapidity, both itself and the new segments which are produced from it are much shorter than they were at an earlier period.

The basal segments have changed again in the manner already described, so that the strongest circles of spines are those on the third, fifth, seventh, eleventh, fifteenth, nineteenth, twenty-third, and twenty-seventh, in addition to which, that on the thirty-first segment has also distinguished itself by an increased development; so that the four darkest segments, which, until now, have immediately followed the last of these fourfold sections, now constitute the last quartet.

This division of the central part of the tails into well-marked divisions, consisting of four segments each, is to my mind a very curious phenomenon. When the sixth and seventh segments divide, the old circle round the apex of the sixth, which is at first more conspicuous than the corresponding circles of the two new segments, tones itself down, until the three closely resemble one another; on the other hand, the apical circle on the segment which in the last stage was the seventh resembles that of the surrounding segments. It, on the contrary, in accordance with some mysterious law, has become more conspicuous; so that the subdivision of the organ into sections of four segments is effected partly, and indeed principally, by the mode of growth, but partly also by the modification, sometimes by diminution, sometimes by development, of the apical circles belonging to old segments.

The thirteenth state lasts for about a week, during which time the insect adds about $\frac{10}{800}$ths to its length.

Fourteenth State.

The rudiments of the wings now cover five-sixths of the metathorax. The antennæ are still of about the same length as the body.

The secondary plates have increased considerably in size on the five intermediate pairs of branchiæ, but the first and last pairs have hitherto remained simple; now, however, the former show at their base a small thumb-shaped lobe (fig. 22).

The lateral tails have grown as before: the last division of four, which is also the darkened portion, includes the thirty-second and three following segments; the fringe extends to the forty-third, beyond which there were at least seven more segments.

The central tail now closely resembles the two lateral ones; it is, however, fringed on both sides, while the lateral tails have on their outer margin only the usual small hairs at the apex of each segment. There were twelve segments beyond the fringe.

Fifteenth State (fig. 14).

This stage commences when the insect has a length of about $\frac{115}{800}$ths to $\frac{120}{800}$ths, and the rudimentary wings reach to the end of the metathorax.

The secondary lobe of the anterior branchiæ reaches almost halfway up the large plate.

The more developed circles are now on the third, fifth, seventh, ninth, thirteenth, seventeenth, twenty-first, twenty-fifth, twenty-ninth, thirty-third, and thirty-seventh segments. The thirtieth and nine following segments are darkened, and the fringe extends to the fifty-first segment. The terminal segments were nine in number, though the organ was imperfect.

In this case it would seem that only the first and third segments of the preceding state

had divided; the sixth and seventh, which were now the eighth and ninth, showed, indeed, traces of commencing subdivision, but they could not yet be considered as constituting joints.

Sixteenth State (fig. 15).

The rudimentary wings cover one-third of the first abdominal segment.

The anterior and second gills are figured in figs. 23 & 24; the former have the secondary lobe slightly longer and narrower than before. As is shown by the figures, its form is quite different from that of the corresponding part of the other branchiæ.

The development of the caudal appendages has proceeded as before, so that the most strongly marked joints are now the third, fifth, seventh, ninth, thirteenth, seventeenth, twenty-first, twenty-fifth, twenty-ninth, thirty-third, thirty-seventh, and forty-first. The thirty-third and six following segments are darkened, and the fringe extends to the fifty-fifth.

In some specimens, however, the forty-fifth, forty-ninth, and fifty-third segments also were more strongly marked than the intermediate ones.

These, indeed, seemed to me (and this was especially the case near the base) to be less distinct than before; while of the newly developing ones it was difficult to draw any line between true segments and joints which were merely indicated.

Seventeenth State (fig. 16).

The wing-cases cover more than half of the first abdominal segment.

The secondary lobes of the anterior gills reach almost to the summit of the primary lobes; their form is, however, almost the same as before.

The divisions into groups of segments, beginning as before with those lying between the ninth and thirteenth, extends now to the sixty-first, where also the fringe terminates. The darkened part extends from the thirty-eighth to the forty-fifth, inclusive, but the first four are very slightly affected.

Thus I have endeavoured, as far at least as my observations at present reach, to describe the different stages through which these larvæ pass, in their progress from birth to maturity. There is, however, one other point, in which these changes remind us rather of growth than of metamorphosis, which is, that the development of the different organs does not seem in all cases to progress with equal rapidity. There are, of course, many differences which are merely the result of injuries; but, on the other hand, there are many which cannot, I think, be so accounted for.

One specimen which had the posterior angles of the mesothorax more developed than those of the metathorax, without, however, covering quite half of that segment, would be considered, if we took these organs as our test, as belonging to the tenth or perhaps the eleventh state. It was $\frac{68}{800}$ths in length. The lateral tail had the most conspicuous circles round the third, fifth, seventh, eleventh, fifteenth, and seventeenth segments, and the fringe reached to the twenty-eighth.

The middle tail in this specimen closely resembled the lateral ones, at least in the

number and position of the "chief segments," and in the development of the fringe, which on some of the segments consisted of five setæ. Some segments of the lateral tails, however, had six. There was no trace of darkening.

Again, a specimen which I began to watch on the 27th of November, when it was apparently in the eighth stage, moulted on the 29th, and again on the 8th of December, when therefore it ought to have been in the tenth state. And, in fact, the length of the central tail, as well as the number of its segments, agreed with the description given in page 74, and the organ differed only in one little point, viz. that the circle round the fifteenth segment was scarcely more developed than its neighbours. In the lateral tails the sixth and seventh segments already showed traces of a subdivision, and the nineteenth segment had already distinguished itself. On the other hand, the posterior angles of the mesothorax were not more produced than those of the following segment. This specimen was $\frac{55}{800}$ths in length.

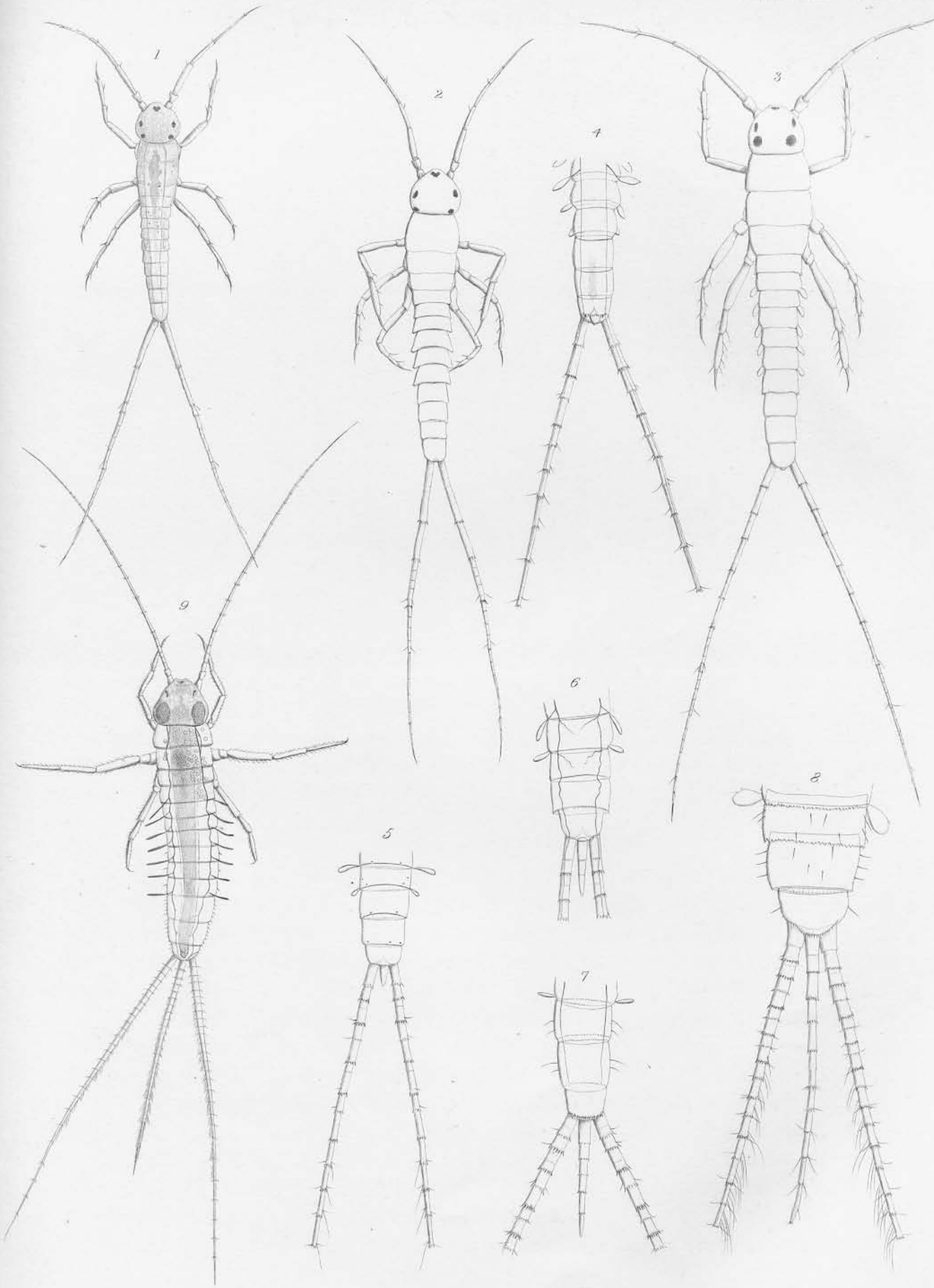
DESCRIPTION OF THE PLATES.

PLATE XVII.

Fig. 1. *Chloëon* in the First State, × 60.
Fig. 2. Outline of *Chloëon* in the Second State, × 60.
Fig. 3. „ „ Third State, × 60.
Fig. 4. Five posterior abdominal segments of *Chloëon* in the Fourth State, × 60.
Fig. 5. Four „ „ „ „ Fifth State, × 60.
Fig. 6. Four „ „ „ „ Sixth State, × 60.
Fig. 7. Three „ „ „ „ Seventh State, × 60.
Fig. 8. Three „ „ „ „ Eighth State, × 60.
(In the last five figures the basal part only of the lateral tails is figured.)
Fig. 9. Larva in the Ninth State, × 30.
(In this figure neither the segments nor the hairs on the antennæ and the tails are quite correct.)

PLATE XVIII.

Fig. 10. Outline of the head, thorax, and first abdominal segment of a specimen in the Tenth State to show the commencement of the wings, × 30.
Fig. 11. Ditto ditto in the Eleventh State, × 30.
Fig. 12. „ „ Twelfth State, × 30.
Fig. 13. „ „ Thirteenth State, × 30.
Fig. 14. „ „ Fifteenth State, × 30.
Fig. 15. „ „ Sixteenth State, × 15.
Fig. 16. „ „ Seventeenth State, × 15.
Fig. 17. „ „ a subsequent State, × 15.
Fig. 18. Antenna of larva in First State, × 125.
Fig. 19. „ „ Second State, × 125.
Fig. 20. „ „ Third State, × 125.
Fig. 21. „ „ Fourth State, × 125.
Fig. 22. Anterior gill of larva in Fourteenth State, × 60.
Fig. 23. „ „ Fifteenth State, × 60.
Fig. 24. Second „ Sixteenth State, × 60.



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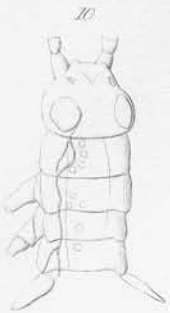
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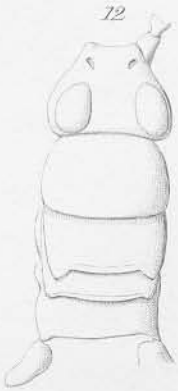
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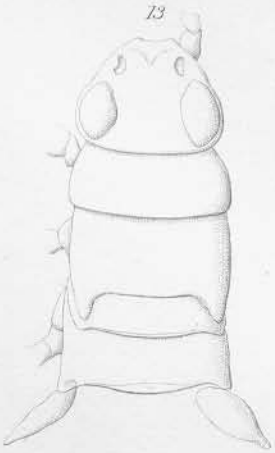
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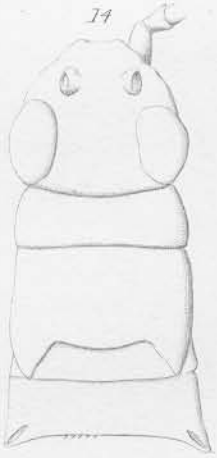
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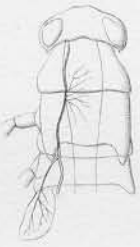
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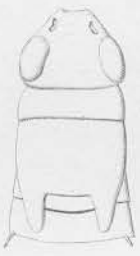
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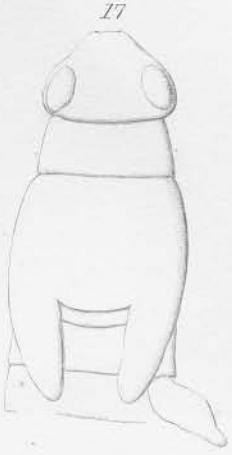
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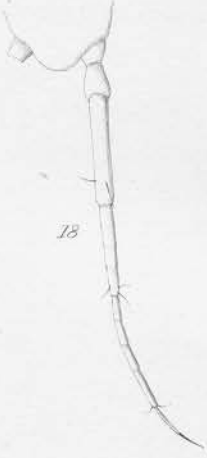
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