XIX. *On the Development of Chloëon (Ephemera) dimidiatum.*

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(Plates LVIII. & LIX.)

PART II.

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THE Linnean Society have done me the honour of publishing, in the 2nd part of the 24th volume of their Transactions, a memoir on the development of a very common freshwater larva—that, namely, of *Chloëon dimidiatum*.

I traced it through seventeen stages, and described the gradual alterations which it underwent. The object of the present communication is, in the same manner, to describe the subsequent and very remarkable changes which take place during the development of the perfect insect.

As will be seen from the Table given at the end of this memoir, the changes of skin during the winter months are separated by longer intervals than is the case in other periods of the year, and sometimes two or even three moults will take place without any material change of form. In December, January, and February there are generally at least 14 (and sometimes as many as 30) days between each moult. Thus a specimen which on the 6th of November entered the 17th stage remained without any material change until the 18th of January, during which period it changed its skin four times, at intervals respectively of 19, 16, 19, and 19 days. My different specimens, however, did not appear to agree exactly as to the number of moults.

Eighteenth State.

The wing-cases now cover the whole of the first abdominal segment, and the length of the body is on an average about $\frac{6}{20}$ of an inch. The segments which compose the antennæ and the caudal appendages continue to increase in number; but it is very difficult to obtain specimens in which these organs are perfect; nor when this is done can the number of segments be very easily determined. Plate LVIII. fig. 1 represents part of the basal portion of one of the caudal appendages, and shows the steps in the process by which the segments are formed. Probably no two observers would exactly agree as to the number of segments which compose one of these organs.

The anterior plate of the anterior branchia is now about as long as the other, and somewhat broader than in the preceding state.

Hitherto all the specimens of the species have resembled one another; but about this period of development the external sexual characters of the males begin to show themselves. Between the two large original eyes we now see indications of a second pair, the rudiments of the two great pillared eyes. In the cast skin we may see that the chitinous head-covering has here undergone a change. The skin is neither divided into the more or less regularly hexagonal facets of the original eye, nor does it present the irregular polygons which mark the upper part of the head; on the contrary, it is marked by a great number of small wedge-shaped dots, which divide it into minute fields, the future facets. These incipient eyes lie close to the others, occupy already a considerable part of the top of the head, and are of an elliptic form.

The second character of the male sex occurs on the underside of the penultimate abdominal segment, the outline of which now presents two very slight projections, which are of importance only as indications of future changes. The females do not appear to present the slightest trace either of these processes or of the pillared eyes.

In the female, the commencement of the ovaries may now be observed, in the form of two cylindrical organs, one on each side of the abdomen. They consist of a central tube with short lateral lobules.

Nineteenth State.

The wing-cases now cover about half of the second abdominal segment, and the insect is about $\frac{1}{3}$ of an inch in length. The antennæ and caudal appendages have again increased in length and in the number of the segments.

The pillared eyes are somewhat more developed, but the facets are still indicated only by the arrangement of the dots. They are about $\frac{2}{7000}$ of an inch in diameter, which is half that of the other eyes.

The anterior plate of the anterior branchia is somewhat longer than before, but there is no great alteration.

The small projections on the underside of the penultimate abdominal segment are rather more developed, but there is no great change in them.

The rudimentary ovaries are somewhat more developed.

Twentieth State.

In this stage, which is the last passed under water, the rudimentary wings cover half of the third abdominal segment, or, in some cases, the whole. The facets of the "pillared eyes," which are characteristic of the male, are still indicated by dots; the facets of the ordinary eyes seemed to me to be more sharply defined than before.

The anterior gills are but little altered.

The antennæ are now far longer than they will be in the next state. This is interesting, as showing that the changes which have taken place in them are not mere stages in the development of the perfect form, but are adapted for some special object, which we have not yet determined. It may be thought that long antennæ, like those of the full-grown larva, would be an encumbrance to flight, and that for this reason they are shortened in the imago; but, on the other hand, it might be said with an equal appearance of probability, that they would be inconvenient for swimming. However this may be, the fact remains, and I was interested to see in what manner the change was effected. This is shown at a glance by Plate LVIII. fig. 2, in which we see that the antenna of the proimago is not only much shorter, but also thinner than that of the present stage, in which it lies like a sword in its sheath. The two basal segments (Plate LVIII. fig. 2 *a*), indeed, are almost filled by the new organ, but this is far from being the case with the thirteen following. In this portion of the antenna (Plate LVIII. fig. 2 *b*), the chitinogenous layer and the soft internal tissues have contracted very much, so that the new antenna lies quite loosely in the old one. It only reaches, however, as far as the fifteenth segment. From this part onwards (Plate LVIII. fig. 2 *c*) the softer tissues of the old antenna are unaltered, they take no part in the formation of the new organ, and when the skin is shed they are cast off with the dead outer layer of the chitine. The connexion between the antenna of the proimago and the tissue of the terminal part of the antenna is shown in Plate LVIII. fig. 3.

The mouth-parts do not essentially differ from the description of them given by Westwood ('On the Modern Classification of Insects,' vol. ii. p. 24).

The *upper lip* (Plate LVIII. fig. 4) is almost quadrangular, rounded off at the free angles, and notched in the middle of the anterior border. It has a number of short hairs along the margin, and a few others scattered over the surface.

The *mandibles* (Plate LVIII. fig. 5) are short, strong, and horny. The free edge may be divided into three very distinct parts. The upper portion is divided into three processes, each of which has two or three teeth. The middle portion is occupied by a tuft of hairs. The basal part under a low power has a molar appearance, but when highly magnified is seen to be set with the curious processes two of which are figured (Plate LVIII. fig. 6), one seen sideways, the other looked at from in front. As usual, the mandibles are slightly unsymmetrical; and one of them has a strong process at the upper end of the molar portion.

The *maxillæ* (Plate LVIII. fig. 7) are short, slightly curved, with two strong teeth, and a row of spines along the upper inner edge. The palpi are rather longer than the maxillæ themselves, and have three joints. According to Westwood the corresponding organ of *E. vulgata* consists of four segments: comparing his figure with my specimens, it seems that the small basal segment is undifferentiated. The two apical segments are also less distinctly separated than in his figure.

The *lower lip* (Plate LVIII. fig. 8) is membranous and deeply quadrifid. The palpi are three-jointed; but the division between the two terminal segments is not strongly marked. Mr. Westwood says that the lower lip is "furnished within with a broad tongue, of which the anterior angles are produced and pilose;" I found, indeed, in addition to the organs already described a three-lobed membranous lip (Plate LVIII. fig. 9), which I presume to be the tongue. It seemed to me, however, to lie in front of the mouth and to be connected, not with the labium, but with the labrum. Possibly it may be homologous with the membranous lobes in the Thysanura, which I have doubtfully suggested to represent a second pair of maxillæ (?).

The small projections on the penultimate abdominal segment of the males are slightly larger, and contain the ends of the two lateral appendages, which towards the end of this period can be distinctly seen through the skin.

The ovaries are two white cylindrical bodies, which occupy the whole length of the abdomen. They consist of a great number of short egg-tubes, each of which is divided into two chambers (Plate LVIII. fig. 10). The upper chamber contains a number of vitellogenous cells; it is elongated and more or less cylindrical in form, terminating at the upper end, as usual, in a delicate string.

The lower chamber is elliptic, and contains numerous oil-globules, some of large size. It has a greenish hue, caused by the presence of numerous small globules.

The Organs of Respiration.

It has been already mentioned that the larvæ in the first three stages possess no respiratory organs whatever. This is a fact so exceptional that, so far as I am aware, no other case is on record. Even the youngest larvæ have hitherto been invariably found to possess tracheæ, and either spiracles or gills, as the case might be. We are apt to be surprised by anything which is unusual; but in reality it appears more difficult to understand why these larvæ should not respire in the same manner as the Crustacea with which they live during the whole of their subaqueous existence, than why they should do so for a short part of it.

Another unusual fact connected with the tracheæ of Chloëon is, that their internal chitinous envelope is not shed with the skin. In ordinary larvæ the inner skin of the tracheæ is shed at each moult, it being drawn out through the spiracles. That the same is not the case in Chloëon depends evidently on the absence of spiracles, so that the shedding would be a physical impossibility. The necessity for a change ceases, however, with the possibility. Where there are open spiracles, dust, &c. must occasionally enter, in spite of the tufts of hair and other ingenious contrivances by which it is to a great extent excluded. At every change of skin, however, all foreign matters are necessarily carried away with the tracheal skin, and the passage is thereby kept free and open. Where, on the other hand, as in the larva of Chloëon, there are no orifices, no foreign matters can possibly enter, and the necessity for changes of skin is perhaps thereby removed.

When, however, the insect changes into the proimago and quits the water, spiracles are formed; and at this moult, for the first time, the inner skin of the tracheæ is cast, as is the case in other insects.

Dr. Hagen has recently published a posthumous memoir by Prof. Rathke *, a translation of which has appeared in the 'Annals and Magazine of Natural History' (ser. 3. vol. ix.)

In this paper Prof. Rathke expresses opinions, as to the manner in which the respiration of insects is carried on, which are very opposite to those which I have advocated in my memoir " On the Tracheæ of Insects," published in the Transactions of this Society for 1860.

Dr. Rathke, after describing the so-called respiratory movements of insects, discusses the function which they perform.

* Schriften der Königl. physik-ökonom. Gesellschaft zu Königsberg, 1861, p. 99.

"The pulsation," he says, "of the dorsal vessel cannot be essentially affected by these movements, as, when they cease for a longer or shorter time, the activity of the dorsal vessel does not stop. This applies also to the action of the digestive organs; for this likewise goes on, and movements (especially peristaltic) of the intestine and malpighian vessels take place, even when the movements of the abdomen cease for some time. There can also be no particular relation between them and the function of the generative organs, as they occur both when the sexual organs are far from maturity and when their activity appears to be purely plastic. There are no other organs in the abdomen of most insects, except the respiratory organs, with which these movements can be connected;" and he concludes, therefore, that the function of their movements is to produce a change of air in the tracheæ, and that, "from the absence of all such phenomena we might conclude that in the pupæ of the above-mentioned insects (Beetles and Hymenoptera) the tracheary respiration is entirely interrupted" *.

But in the paper above mentioned, I have shown that the mode in which the tracheæ branch offers no support to the idea of any circulation of air, while the fact that they end in long blind extremities seems to be fatal to any such hypothesis. Under these circumstances, it occurred to me, as indeed had been suggested long before by Dr. Graham, that the interchange of air was effected by virtue of the diffusion of gases. I see no reason to change this opinion, which, moreover, receives very strong support from the arrangement of the respiratory organs of the Chloëon-larva and other aquatic larvæ which respire by means of gills. Here there are no external openings, consequently there can be no inspiration or expiration of air; and yet it is evident that the respiration is not interrupted.

I will not deny that in aërial insects a partial change of the air in the larger tracheæ may be effected by the "respiratory" movements, nor will I assert that there are "any other organs in the abdomen" . . . . . . with which these movements can be connected. But it seems very possible that they may tend, and be intended, to assist the weak "dorsal vessel" in producing the circulation of the blood.

In considering the gills, it is remarkable how small a portion of the surface is occupied by the tracheæ. Plate LVIII. fig. 11 represents a portion of the anterior gills; and it will at once be seen how large a part of the surface is apparently wasted. This is a fair example, and quite as richly supplied with air-vessels as is usual. It was copied immediately after the death of the insect, and before any material change had taken place. In younger larvæ it might be said that the organ was partially embryonic, and that the large extent of membrane was in preparation for a richer network of tracheæ. As, however, we have now reached the definite condition of these gills, which will be thrown off at the next change of skin, this argument does not apply. Nor is this an exceptional case; the same poverty, if I may use the expression, is visible in the corresponding organs of other water-insects, and may perhaps be taken as collateral evidence that the true *modus operandi* of these organs is not yet perfectly understood—and the more so if we bear in mind the richness in blood-vessels of the lungs of higher animals.

* Ann. & Mag. Nat. Hist. ser. 3. vol. ix. pp. 95, 105.

Possibly one principal function of the branchiæ is to produce constant currents, thereby bringing fresh supplies of water into contact with the general surface of the skin, through which doubtless much of the respiration is carried on.

On the other hand, there are species to which (as, for instance, is the case with *Ephemera vulgata*) this argument does not apply.

According to Rathke, "the muscles by which these movements are produced are exceedingly simple. Each segment which takes part in it is furnished only with a single pair of muscles for this purpose, each of which is attached by one end to the lateral wall, and by the other to the dorsal wall or plate, in both places close to the soft parts of the cutis"*.

In the same manner Chabrier † tells us that the wing-muscles do not (except apparently among the Libellulidæ) act *directly* on the wings, "mais ils les meuvent par l'intermédiaire du dorsum et par d'autres leviers particuliers." Some light seems to be thrown on this remarkable fact by the above-mentioned statement of Rathke; and the movement of the branchiæ in aquatic larvæ forms a connecting link between the two, and throws some light on the curious arrangement of the muscles observed by Chabrier.

The Digestive Organs.

The œsophagus is very short indeed, and expands immediately behind the head into the stomach, for which there is plenty of room even in the thoracic segments, owing to the weakness of the legs and the smallness of the muscles by which they are moved. The ilium is quite short and well rounded. The rectum is rather longer, and cylindrical. The Malpighian vessels are numerous and short. They open as usual into the posterior end of the stomach. According to Burmeister the Neuroptera have six Malpighian vessels; in this species they are, however, more numerous and of a somewhat peculiar form, consisting of two parts, which are about equal in length. The distal portion consists of a thin cylindrical tube. The other half is shaped like a long club, to the broad end of which the cylindrical tube or efferent duct is attached. Swammerdam (Bib. Nat. plate xv. fig. 5), who is quoted by Ramdohr (Verdauungswerkzeuge der Insekten p. 151), does not figure or mention any Malpighian vessels. It is true that his observations did not refer to the same species as mine; but it seems unlikely that the different species of *Ephemera* should differ from one another in a point of so much importance. The Malpighian vessels are formed of nucleated cells in the usual manner. Under the action of acetic acid, they become quite transparent.

The food consists principally of minute Diatomaceæ. Swammerdam, indeed, says that the larvæ of the Ephemeridæ feed on mud; but this is probably a mistake arising from the small size of the Diatoms and the low powers used by him. Still it is quite possible that it may be true of the species examined by him. Other species, again, according to Pictet, are insectivorous.

* *Loc. cit.* p. 83.

† Vol des Insectes, p. 33.

Proimago.

One morning in June I observed a full-grown larva, which had a glistening appearance, owing to the presence of a film of air under the skin. I put it in my microscope, under a low power; and then, having added a drop more water with a pipette, I put the instrument down, and looked through the glass. To my astonishment, the insect was gone, and an empty skin only remained. I then caught a second specimen in a similar condition, and put it under the simple microscope, hoping to see it come out. Nor was I disappointed: very few moments had elapsed when I had the satisfaction of seeing the thorax open along the middle of the back; the two sides turned over, the proimago literally walked out of itself, unfolded its wings, and in an instant flew up to the window.

Several times since, I have had the pleasure of witnessing this wonderful change; and it is really extraordinary how rapidly it takes place; from the moment when the skin first cracks, not ten seconds are over before the insect has flown away. For some little while before the change the larva is rather helpless; but this is of the less importance, because this larva is not obliged, like many others, to leave the water before it emerges. Owing to the production of air between the old and new skins, it naturally comes to the surface; and it is probable that the quantity of air between the folds of the wings brings the back of the thorax uppermost. When the larval skin has burst and folded itself back, it acts for the moment as a raft.

The antennæ are as in Plate LVIII. fig. 2 *a* & *b*; they consist of a basal portion formed by two segments, and succeeded by an unjointed whiplike part, which has a very curious appearance, the whole surface being covered by small but well-marked ridges, which include small angular areas. Zaddach maintains that the antennæ of the imago are not homologous with those of the larvæ; but it is evident that in *Ephemera*, at least, there is no such difference.

The pillared eyes of the male are brown, but each has a pale band running round it just below the crown. The three ocelli have not changed much in appearance. On the top of the head, between the two large eyes, the male has two rounded eminences, which occupy the places where two new eyes will, in the perfect imago, make their appearance.

The feet of all the three pairs are similar (see Plate LIX. fig. 12, which represents the first pair). The tarsi are four-jointed; the last bears a soft rounded pad, which might be described as a fifth tarsal segment. In the two posterior pairs of legs, the third tarsal segment is shorter than the others. The claw is quite small, and does not project beyond the terminal pad. There are no long hairs on the legs, which are covered, however, by short ones; those on the tarsus are stiff, and almost deserve the name of spines. The skin of the tarsal segments is thrown into small ridges like those on the antennæ.

The wings are of a dusky hue. They are covered by minute hairs, and are fringed along the hinder edge (Plate LIX. fig. 13). This appears to be the case also with most, if not all, of the other species of the group.

The caudal filaments are about $\frac{1}{2}$ an inch in length; near the base they are $\frac{1}{180}$ of an inch in thickness; but they gradually taper to the free end, where they are only $\frac{1}{600}$, ending finally in a blunt point. The segments at the base are about $\frac{1}{150}$ of an inch in length, but they increase somewhat towards the free end. There are no longer any fringes; but the whole surface is covered with short, equidistant, strong, pointed hairs. The middle tail of the larva is represented by a short conical appendage.

The sexual appendages of the male (Plate LIX. fig. 14) are four-jointed. The two basal segments are short and broad; the third is cylindrical, $\frac{1}{80}$ of an inch in length. The terminal segment is small. The whole organ is covered with minute hairs. These organs are absent in the female.

Imago.

The two great pillared eyes (Plate LIX. fig. 15) at once distinguish the male from the female. In the latter they are entirely absent: in the former they occupy almost the whole top of the head; and the larval eyes, which do not appear to have undergone any great change in appearance, are thrown entirely to the side. The pillared eyes are facetted only on the flat summits. The antennæ resemble those of the proimago.

The anterior legs of the male (Plate LIX. fig. 16) are elongated, though not so much so as in some other species. The tarsal segments, which are four in number, decrease in length from the first to the last, which bears a single claw. The two posterior pairs more closely resemble those of the proimago, and, like them, have the third segment shorter than the terminal one. The third pair terminates in a pad and a claw (Plate LIX. fig. 17). The skin of the legs resembles that of the proimago.

The wings are paler and more delicate than those of the proimago. There are no hairs, nor is there any fringe on the hinder margin (Plate LIX. fig. 18); but the nervures are more sharply defined. The shape of the wings and the arrangement of the nervures has undergone little change.

It is difficult to understand the cause of the differences which exist between the wings of the proimago and those of the imago. They are not confined to this species, but appear to be general to the whole group. In *Palingenia virgo*, indeed, the posterior margin bears a row of hairs; but even in this species they are quite unlike those of the proimago.

The two tails are of considerable length, and consist of a number of segments. They are near the base, about $\frac{1}{360}$ of an inch in thickness, and each segment has a length of from $\frac{1}{180}$ to $\frac{1}{120}$ of an inch. Instead of the long fringes which were present in the larvæ, and which may be supposed to have been of assistance in swimming, the whole surface of the caudal appendages in the imago is covered with short, stiff, pointed hairs, which are all of nearly the same size.

The appendages are pale in colour; but the joints are dark brown, which gives them a ringed appearance. Sometimes every second joint is darker than the rest.

The perfect insect makes its appearance in June.

In my previous memoir I referred the above insect, on the authority of Mr. Walker, to *Chloëon dimidiatum*. Since then I have also forwarded specimens to Mr. M'Lachlan, who has devoted much time to the examination of this family, and who confirms the opinion of Mr. Walker. The group, however, much wants a careful revision.

Curtis's description of *Chloëon dimidiatum* is as follows:—" Length 3 lines. Castaneous brown; collar with an ochreous dot on each side; abdomen, especially at the base, banded with ochre; filaments very long and white, remotely dotted with black; legs straw-colour; nervures of wings very faint."—*Phil. Mag.* 1834, p. 121.

Having thus traced up, step by step, the history of this insect from a period when it is no more than $\frac{1}{40}$ of an inch in length until its appearance in the perfect state, I will, in conclusion, say a few words on the general subject of insect-metamorphoses. The two points to which I would particularly call the attention of entomologists are:—

First, the gradual changes which are undergone by these larvæ. We shall, I believe, find the same to be the case with other larvæ of the homomorphous series of insects.

And, secondly, the fact that many of these changes bear no reference to the ultimate form of the insect, but are connected with the conditions in which the larva itself is placed.

Moreover I have called attention to the fact that there are certain differences even between the proimago and the imago. These, indeed, are not extensive; the mere presence or absence of minute hairs on the surface of the wing, and of a fringe on its posterior margin, may not seem in themselves at first sight to be points of much interest or importance; when, however, they are taken in conjunction with the changes which occur in the antennæ, with the formation and subsequent disappearance of the branchiæ and middle tail, as well as with other similar facts which have been recorded in this memoir, they appear to suggest considerations of much interest.

The larvæ of insects are generally regarded as being nothing more than immature states, as stages in the development of the egg into the imago; and this might more especially appear to be the case with those insects in which the larvæ offer a general resemblance in form and structure (excepting of course so far as relates to the wings) to the perfect insects. Nevertheless we see that this would be a very incomplete view of the case. The larva and pupa undergo changes which have no relation to the form which they will ultimately assume. With a general tendency, as regards size and the production of wings, to this goal, there are combined other changes bearing reference only to their existing wants and condition.

Nor is there in this, I think, anything which need surprise us. External circumstances act on the insect in its preparatory states as well as in its perfect condition. Those who believe that animals are susceptible of great, though gradual, change through the influence of external conditions, whether acting, as Mr. Darwin has suggested, through natural selection, or in any other manner, will see no reason why these changes should be confined to the mature animal. And it is evident that creatures which, like the majority of insects, live during different periods of their existence in very different circumstances, may undergo considerable changes in their larval organization, in consequence of forces acting on their larval condition, not, indeed, without affecting, but certainly without affecting to any corresponding extent, their ultimate form.

We can in this manner, I think, understand those cases in which animals, very similar in their mature condition, are very unlike in their earlier stages.

The question still arises, Why do insects pass through metamorphoses? Messrs. Kirby and Spence tell us that they "can only answer that such is the will of the Creator" *,—

* 'An Introduction to Entomology,' sixth edition, vol. i. p. 61.

which, however, is rather a general confession of faith than an explanation of metamorphoses. And this they appear to have felt themselves; for they immediately proceed to make a further suggestion. "Yet one reason," they say, "for this conformation may be hazarded. A very important part assigned to insects in the economy of nature, as I shall hereafter show, is that of speedily removing superabundant and decaying animal and vegetable matter. For such agents an insatiable voracity is an indispensable qualification, and not less so unusual powers of multiplication. But these faculties are in a great degree incompatible; an insect occupied in the work of reproduction could not continue its voracious feeding. Its life, therefore, after leaving the egg, is divided into three stages."

But there are some insects, as, for instance, the Aphides, which certainly are not among the least voracious, and which eat and breed at the same time. There are also many scavengers among other groups of animals, such, for instance, as the dog, the pig, and the vulture, which undergo no metamorphosis.

It is certainly true that, as a general rule, growth and reproduction do not occur together; and it follows, almost as a necessary consequence, that in such cases the first must precede the second. But this has no immediate connexion with the occurrence of metamorphoses. The question is, not why an insect does not generally begin to breed until it has ceased to grow, but why, in attaining to its perfect form, it passes through such remarkable changes. And in addition to this, we must consider, first, the sudden and apparently violent nature of these transitions, and, secondly, the immobility of the animal in its pupa state; for undoubtedly the quiescent and deathlike condition of the pupa is one of the most remarkable characteristics of insect-metamorphosis.

First, then, the necessity for change depends on the fact that most insects leave the egg in a very early condition*. The Orthoptera, indeed, and other homomorphous insects, are hatched in a more advanced form, and consequently undergo fewer subsequent changes than is the case with other insects. Those processes, however, of evolution which take place in the egg itself attract comparatively little attention, even among entomologists.

We may now pass to the second part of the subject—that is to say, the apparently sudden and abrupt nature of the changes which insects undergo. I say "apparently," because the changes in the internal organs, though rapid, are in reality gradual; and even as regards the external form, though the metamorphosis may take only a few minutes, this is but the change of outer skin—the drawing away, as it were, of the curtain; and the new form which then appears has been in preparation for days or, perhaps, weeks before.

Swammerdam, indeed, supposed (and his view was adopted by Kirby and Spence†) that the larva contained within itself "the germ of the future butterfly, enclosed in what will be the case of the pupa, which is itself included in the three or more skins, one over the other, that will successively cover the larva." This is entirely a mistake; but it *is* true

* And this, again, is probably owing to the fact that the amount of nourishment in the egg is insufficient to carry the insect to maturity.

† *Loc. cit.* p. 55.

that, if you examine a larva shortly before it becomes a pupa, you will find that the skin is loose, and that within it the future pupa may be traced. In the same manner, if you examine a pupa which is about to disclose the butterfly, you will find the future insect, soft indeed and imperfect, but still easily recognizable, lying more or less loosely within the pupa-skin. More than one such inner skin, however, is never present.

One fundamental difference between an insect and a vertebrate animal is, that whereas in the latter, as for instance in ourselves, the muscles are attached to an internal bony skeleton, in insects no such skeleton exists. They have no bones, and their muscles are attached to the skin. Hence the necessity for the hard and horny dermal investment of insects, so different from the softness and suppleness of our own skin.

Moreover the result is, that without a change of skin a change of form is impossible. The chitine, or horny substance, forming the outside of an insect is formed by a layer of cells lying beneath it, and, once formed, cannot be altered. From this it follows that every change of form is necessarily accompanied by a change of skin.

In some cases, as for instance in *Chloëon*, each change of skin is accompanied by a small change of form, and thus the perfect insect is more or less gradually evolved. In others, as for instance in Caterpillars, several changes of skin take place without any alteration of form, and the change, instead of being spread over many, is confined to the last two moults.

Very little consideration will afford us an explanation of this difference. The mouth of the Caterpillar is provided with a pair of strong jaws, fitted to eat leaves; and the digestive organs are adapted for this kind of food.

On the contrary, the mouth of the butterfly is suctorial; it has a long proboscis, beautifully adapted to suck the nectar from flowers, but which would be quite useless, and, indeed, only an embarrassment to the larva. The digestive organs also are adapted for the assimilation, not of leaves, but of honey. Now it is evident that if the mouth-parts of the larva were gradually metamorphosed into those of the perfect insect, through a number of small changes, the insect would in the meantime be unable to feed, and liable to perish of starvation in the midst of plenty.

On the contrary, in the Orthoptera and, as a general rule, among those insects in which the changes are gradual, the mouth of the so-called larva resembles that of the perfect insect, and the principal difference is in the presence of wings.

Similar considerations throw much light on the nature of the chrysalis or pupa state—that remarkable period of death-like quiescence which is one of the most striking characteristics of insect-metamorphosis. The comparative quiescence of the pupa is mainly owing to the rapidity of the changes going on in it.

In the chrysalis of a butterfly, for instance, not only, as has been already mentioned, are the mouth and digestive organs undergoing change, but the same is the case with the muscles. The powerful ones which move the wings are in process of formation; and even if they were in a condition favourable to motion, still the nervous system, by which the movements are set on foot and regulated, is also in a state of such rapid change that it could scarcely act.

Finally, from the metamorphoses of insects we pass naturally to that most remarkable phenomenon which is known as the "Alternation of Generations," for the first systematic view of which we are indebted to my eminent friend Prof. Steenstrup.

I have always felt it very difficult to understand why any species should have been created in this double character; nor, so far as I am aware, has any explanation of the fact yet been attempted. Yet insects offer, in the metamorphoses which they go through, a phenomenon not altogether dissimilar, and give a clue to the manner in which alternations of generations may have originated.

The Caterpillar owes its difference from the Butterfly to the early stage at which it leaves the egg; but its actual form is mainly due to the influence of the conditions in which it lives. If the Caterpillar, instead of changing into one Butterfly, produced several Butterflies, we should have an instance of alternation of generations. Until lately, however, we knew of no such case; each larva produced one imago, and that not by generation but by development. It has long been known, indeed, that there are some species in which certain individuals remain always apterous, while others acquire wings. Many entomologists, however, regard these abnormal individuals as perfect though wingless insects; and therefore, though these cases appear to me to deserve more attention than they have yet received, I shall not build any argument on them.

Recently, however, Prof. Wagner, of Kazan, has discovered that, among certain small gnats, the larvæ do not themselves directly produce the perfect insect, but give rise to other larvæ, which undergo metamorphoses of the usual character, and eventually become gnats. His observations have been confirmed, as regards this main fact, by other naturalists; and there can, I think, be no doubt that they are in the main correct.

Here, then, we have a distinct case of alternation of generations, as characterized by Steenstrup. Probably other cases will be discovered in which insects undeniably in the larval state will be found to be fertile. Nay, it seems to me possible, if not probable, that some larvæ which do not now breed, in the course of ages may come to do so.

If this idea is correct, it shows us how the remarkable phenomenon known as alternation of generations may have originated. At any rate, we find among insects every mode of development, from simple growth on the one hand, to well-marked alternation on the other. In the wingless species of Orthoptera there is little difference, excepting in size, between the young larva and the perfect insect. The growth is as simple and gradual as in any other animal; and the creature goes through nothing which would, in ordinary language, be called a metamorphosis. In the majority of Orthoptera the presence of wings produces a marked difference between the larva and the imago. The habits, however, are the same throughout life, and consequently the action of external circumstances affects the larva in the same manner as the perfect insect.

This is not the case with the Ephemeridæ. The larvæ do not live under the same conditions as the perfect insects; external forces accordingly affect them in a different manner; and we have seen that they pass through some changes which bear no reference to the form of the perfect insect: these changes, however, are for the most part very gradual. The caterpillars of Lepidoptera have even more extensive changes to undergo; the mouth of the larva, for instance, is remarkably unlike that of the perfect insect. A change in this organ, however, could hardly take place while the insect was still growing fast, and consequently feeding voraciously. Nor, even if the change could be thus effected, would the mouth, in its intermediate stages, be in any way fitted for biting and chewing leaves. The same reasoning applies also to the digestive organs. Hence the caterpillar undergoes little, if any, change, except in size, and the metamorphosis is concentrated, so to say, into the last two moults. The changes then become so rapid and extensive, that the intermediate period is necessarily one of quiescence.

Owing to the fact that the organs connected with the reproduction of the species come to maturity at a late period, larvæ are generally incapable of breeding. There are, however, some flies which have viviparous larvæ, and thus offer a typical case of alternation of generations, owing to the early period of leaving the egg, and the action in many cases of external circumstances on the larva different from those which affect the mature form.

Thus, then, we find among insects every gradation, from the case of simple growth to that of alternation of generations; and we see how from the single fact of the early period at which certain animals quit the egg, we can account for the metamorphoses they go through, and the still more remarkable phenomenon that, among many of the lower animals, the species is represented by two very different forms. We may even, from the same considerations, see reason to conclude that this phenomenon may in the course of ages become still more common than it is at present. As long, however, as the external organs arrive at their mature form before the internal generative organs are fully developed, we have cases of metamorphosis; but if the reverse is the case, then alternation of generations often results.

The same considerations throw much light on the remarkable fact, that in alternation of generations the reproduction is always agamic in the one form. This results from the fact that impregnation requires the perfection both of the 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 result in those species only which have the power of agamic multiplication.

Moreover it is evident that we have in the animal kingdom two kinds of dimorphism.

The term has usually been applied to those cases in which animals or plants present themselves at maturity under two different forms. The different forms of Ants and Bees afford us familiar instances among animals; and among plants the remarkable case of the genus *Primula* has recently been worked out with his usual ability by my friend Mr. Darwin. Even more recently he has made known to us the still more remarkable phenomenon afforded by the genus *Linum*, in which there are three distinct forms, and which therefore offers an instance of polymorphism*.

The other kind of dimorphism or polymorphism differs from the first in resulting from the differentiating action of external circumstances, not on the mature, but on the young individual. The different forms, therefore, stand towards one another in a relation of succession. In the first case the chain of being divides at the extremity; in the other it is composed of dissimilar links. Many cases of dimorphism under this second form have been described under the name of alternation of generations.

* Indeed all animals in which the sexes are distinct are truly dimorphic.

The term, however, has met with much opposition, and is clearly inapplicable to the differences exhibited by insects in different periods of their life. Strictly speaking, the phenomena are very frequently not alternate, and, in the opinion of many eminent naturalists, they are not cases of generation at all*.

In order, then, to have some name for these remarkable phenomena, and to distinguish them from those cases in which the *mature* animal or plant is represented by two or more different forms, I think it would be convenient to retain for these latter exclusively the terms dimorphism and polymorphism; and those cases in which animals or plants pass through a succession of different forms might be distinguished by the name of dieidism or polyeidism.

The conclusions, then, which I think we may draw from the preceding and other considerations, are:—

1st. That the occurrence of metamorphoses arises from the immaturity of the contion in which some animals quit the egg.

2nd. That the form of the larva in insects, whenever it departs from the original vermiform type, depends in great measure on the conditions in which it lives. The external forces acting upon it are different from those which affect the mature form; and thus changes are produced in the young which have reference to its immediate wants, rather than to its final form.

3rd. That metamorphoses may therefore be divided into two kinds, developmental and adaptational.

4th. The apparent abruptness of the changes which insects undergo arises in great measure from the hardness of their skin, which permits no gradual alteration of form, and which is itself necessary in order to afford sufficient support to the muscles.

5th. The immobility of the pupa or chrysalis depends on the rapidity of the changes going on in it.

6th. 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.

7th. 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.

8th. 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.

9th. The dimorphism thus produced differs in many important respects from the

* "There is no such thing as a true case of 'alternation of generations' in the animal kingdom; there is only an alternation of true generation with the totally distinct process of gemmation or fission."—*Huxley on Animal Individuality*, Ann. & Mag. of Nat. Hist., June 1852.

dimorphism of the mature form which we find, for instance, in ants and bees; it would therefore be convenient to distinguish it by a different name; and I have ventured to suggest the terms Dieidism and Polyeidism.

The same considerations explain the remarkable fact that in alternation of generations the reproduction is 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.

Time of moulting.	State.	No. of days.	Time of moulting.	State.	No. of days.
Specimen No. 1.			Specimen No. 2.		
Captured Sept. 8	4th		Captured Aug. 17	9th	
Moulted „ 9	5th		Moulted „ 21	10th	
„ „ 11	6th	2	„ „ 23	11th	2
„ „ 15	7th	4	„ „ 30	12th	7
„ „ 18	8th	3	„ Sept. 6	13th	7
„ „ 21	9th	3	„ „ 10	14th	4
„ „ 24	10th	3	„ „ 15	15th	5
„ „ 27	11th	3	„ „ 21	..	6
„ „ 30	12th	3	„ „ 27	16th	6
During October I was for	some days away from	home.	„ Oct. 4	..	7
„ Oct. 24	13th		„ „ 13	..	9
„ Nov. 2	„	9	„ Nov. 6	17th	24
„ „ 17	14th	15	„ „ 25	„	19
„ Dec. 8	„	21	„ Dec. 11	„	16
„ „ 24	15th	16	„ „ 30	..	19
„ Jan. 7	„	14			
„ „ 23	„	16			
„ Feb. 8	16th	16	„ Jan. 18	Rudiments of wings covering half the 1st abdominal segment.	19
„ „ 18	„	10			
„ March 1	17th	11			
„ „ 10	„	9	„ Feb. 4	„	17
„ „ 20	„	10	„ „ 22	„	18
			„ March 6	„	12
„ „ 30	Rudiments of wings covering much of the 1st abdominal segment.	10	„ „ 24	19th	18
„ April 10	„	11	„ April 1	Rudiments of wings covering $\frac{2}{3}$ of the 2nd abdominal segment.	8
„ „ 29 ?	Rudiments of wings covering much of the 3rd abdominal segment.	?	„ „ 10	Rudiments of wings covering $\frac{3}{4}$ of the 3rd abdominal segment.	9
„ May 14	Proimago.				

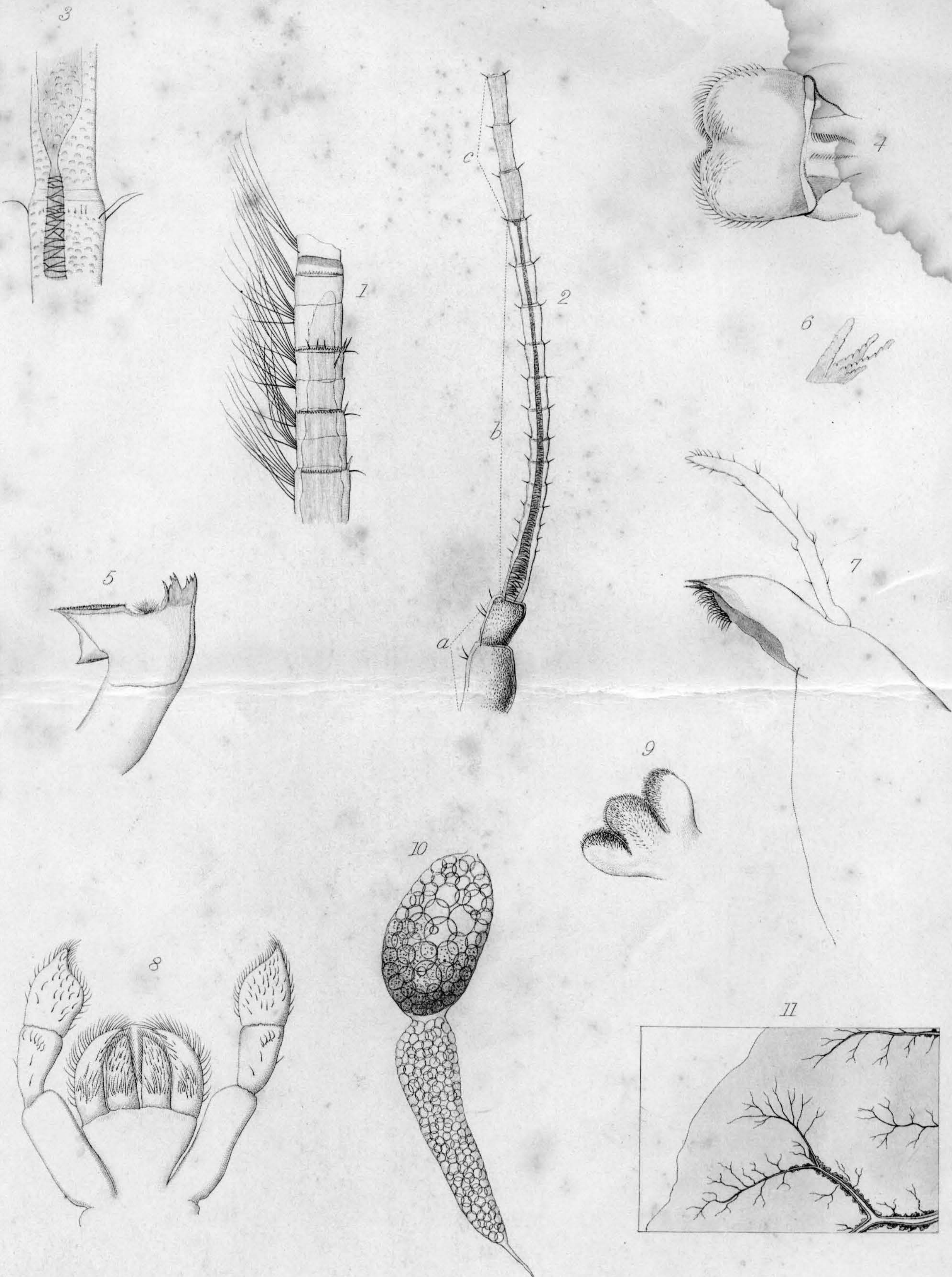
DESCRIPTION OF THE PLATES.

Plate LVIII.

Fig. 1. Basal part of one of the caudal processes, showing the mode of reproduction, × 60.
Fig. 2. Basal portion of the antenna in the 20th state, showing, within, that of the proimago, × 60.
Fig. 3. Portion of the above, × 250.
Fig. 4. Upper lip of full-grown larva, × 60.
Fig. 5. Mandible, × 60.
Fig. 6. Processes of ditto, × 250.
Fig. 7. Maxilla, × 60.
Fig. 8. Labium, × 60.
Fig. 9. Tongue?, × 60.
Fig. 10. Egg-tube, × 250.
Fig. 11. Portion of abdominal process, × 250.

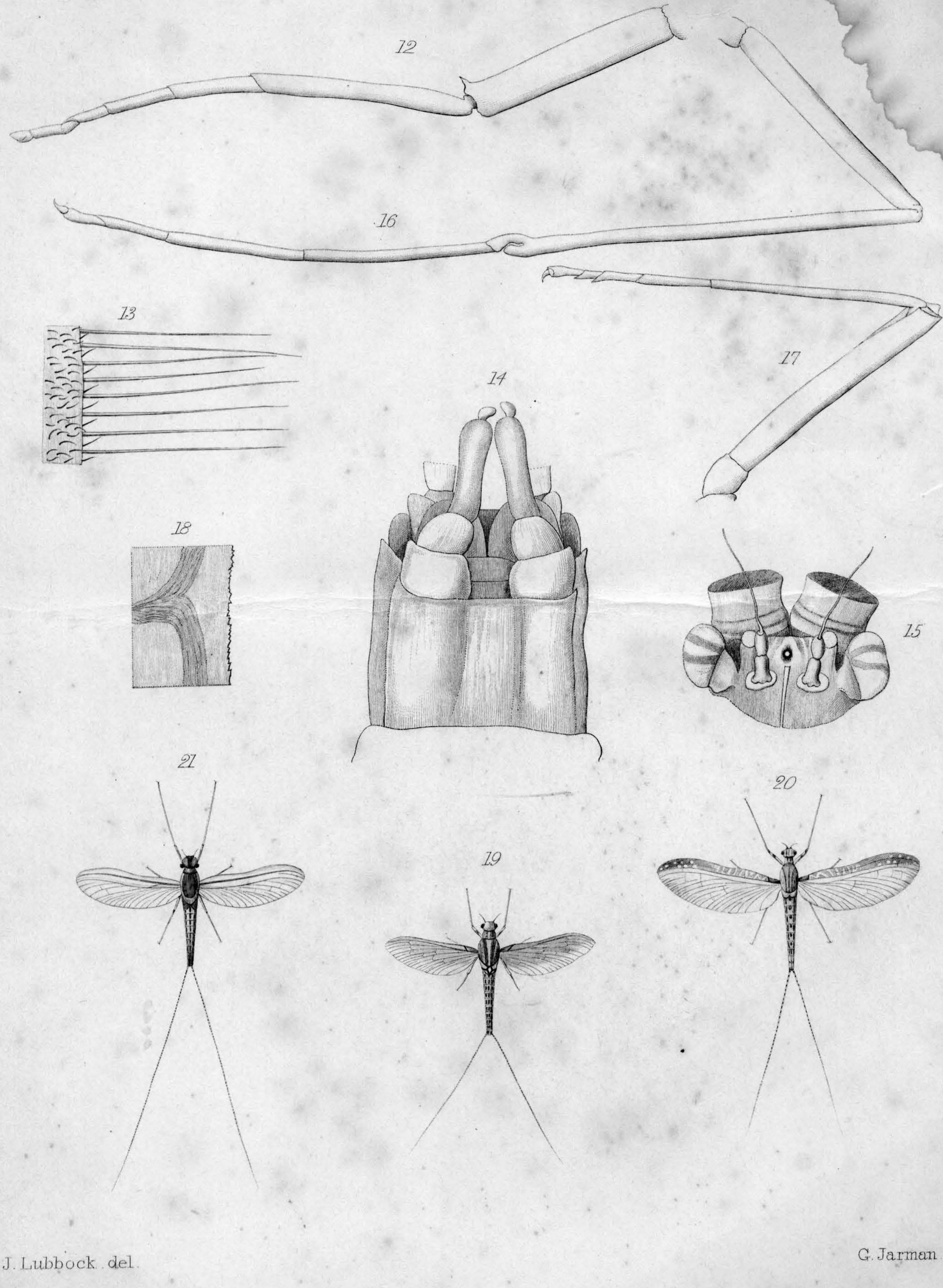
Plate LIX.

Fig. 12. Fore leg of proimago, × 30.
Fig. 13. Margin of wing of ditto, × 250.
Fig. 14. Posterior segment of the abdomen in the male, seen from below, × 60.
Fig. 15. Head of imago, × 30.
Fig. 16. Fore leg of imago, × 30.
Fig. 17. Hind leg of ditto, × 30.
Fig. 18. Margin of wing of imago, × 250.
Fig. 19. *Chloë* (Diptera): proimago, female, after Pictet, about half the natural size.
Fig. 20. *Chloë* (Diptera): imago, female.
Fig. 21. *Chloë* (Diptera): imago, male.



J. Lubbock del.

G. Jarman sc.



J. Lubbock. del.

G. Jarman. sc.