V. *The External Morphology of the Lepidopterous Pupa: its Relation to that of the other Stages and to the Origin and History of Metamorphosis.*—Parts I.—III. By EDWARD B. POULTON, M.A., F.R.S., F.L.S., of Keble and Jesus Colleges, Oxford.

(Plates XX. & XXI.)

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INTRODUCTION.—The observations recorded in this paper and those which will follow it were begun in the autumn of 1883, and have been continued intermittently up to the present date. The remarkably characteristic form of the external generative organs in both sexes of the pupæ of several British Sphingidæ first directed my attention to the subject. For a long time I hoped that it would be possible to bring out a monograph dealing with the whole question. The length of time which must have elapsed before anything like a complete treatise could have been produced, and the difficulties attending the only suitable form of publication, as a quarto volume, have induced me to take the advice long ago offered by Prof. E. Ray Lankester, and to bring out a series of papers dealing successively with the various morphological features which can be detected on the surface of the Lepidopterous pupa.

In the meantime my friend Mr. W. Hatchett Jackson, Deputy Linacre Professor of Human and Comparative Anatomy in the University of Oxford, has also been studying

one part of the same subject, viz. the external reproductive organs, although the principal part of his investigation has been concerned with the development of the internal organs. Under these circumstances we both agreed that it would be advisable to publish at the same time and through the same channel. The two papers will thus supplement each other—Mr. Jackson's supplying the details of internal anatomy at various stages of development, mine dealing with the external organs in a number of different species. For this reason the first paper of my series is chiefly concerned with the external reproductive organs. I may add that I had intended to work out the internal anatomy by means of sections and dissections, but, in the press of other work, such an investigation might have caused the indefinite postponement of publication; I am therefore especially pleased that Mr. Jackson should have been led to undertake this inquiry.

The Names of the various Appendages &c. of the Pupa.—It has been the custom hitherto to speak and think of the various parts of the pupa as if they were mere cases for the corresponding part of the imago. Thus the terms *ophthalmotheca*, *pterotheca*, *ceratotheca*, *podotheca*, &c. have been applied to the parts within which the imaginal eyes, wings, antennæ, legs, &c. are respectively contained. The investigations which will be described in this series of papers have convinced me that these terms and ideas are entirely erroneous. Such appendages or organs represent parts of the pupa, and I shall speak of them as pupal eyes, wings, antennæ, legs, &c. Although modified in shape, so that the imaginal organs can be contained within them, their form and structure are not identical with the latter, but are far more ancestral; they are remnants of a time when the last stage of metamorphosis in the ancestors of Lepidoptera was something very different from a butterfly or moth. The old terminology obscured the fact that the pupa has a morphological meaning of its own, and that traces of an extremely remote past can be deciphered by the study of its structure.

It is well known that the pupa can be dissected out of the skin of a mature larva many hours before the occurrence of normal pupation. Under these circumstances the pupal appendages are not soldered down by a thick coat of varnish, which hardens on exposure to the air, but stand out freely as evident legs, wings, &c. These appearances are nevertheless unaccountably described by many authors as the appendages of the *perfect insect*. Thus Swammerdam points out the method by which the pupa can be freed from the larval skin in *Pieris brassica*; he then says:—"This done, it is clearly and distinctly seen that within this skin of the caterpillar a perfect and real butterfly was hidden" ('Book of Nature,' ii. 26). This erroneous view is corrected by Sir John Lubbock*.

Professor Weismann's great discovery that the contents of the pupa of Diptera break down (histolysis) into nutrient fluids and lowly differentiated units, from which the imago is subsequently built up by a process akin to embryological development, has an important bearing upon the subject. If we examine a section of a pupal antenna or leg (in Lepidoptera) we shall find that there is no trace of the corresponding imaginal organ until shortly before the emergence of the imago. In the numerous species with a long

* 'Origin and Metamorphoses of Insects,' p. 67.

pupal period the formation of imaginal appendages within those of the pupa is deferred until very late, and then takes place rapidly in the lapse of a few weeks. This also strengthens the conclusion that such pupal appendages are not mere cases for the parts of the imago, inasmuch as these latter are only contained within them for a very small proportion of the whole pupal period.

A Classification of the various Features constituting the External Morphology of the Pupa.—Anticipating the results of investigations to be described in future papers, we shall find that the features which can be made out on the surface of a pupa may be grouped, according to their origin, under four chief heads:—

I. The first of these heads includes the essential and ancestral features derived from stages of a more ancient and continuous form of metamorphosis, and probably in some cases also transmitted from the ultimate, sexually mature, stage of a still earlier and simpler method of development. To this division belongs the general structure of the body: its segments, spiracles, limbs, wings, and probably antennæ; but not the details of these. Also, more specially, the pupal external generative organs and the crescent-shaped compound eye.

II. The second head includes those modifications of the general structure which are due to the development of a very different form within it. These modifications have determined the special form and, in some cases, sculpture of the wings, limbs, and antennæ, and have probably taken a much larger share in producing the present form of the pupal maxillæ. Inasmuch as a modification once wrought upon the pupa will often outlive the imaginal structure which caused it, we have some interesting proofs of former structural arrangements in the imago. These modifications due to the imago may be classified: (α) Those details which are common to a large number of pupæ, and in which the imaginal structures fit the corresponding parts of the pupa. This includes the vast majority of the details arranged under the second head. (β) Those obviously recent and exceptional modifications of the pupal structure which have been formed to accommodate a rapidly increasing imaginal structure. This includes the development of special outgrowths to contain the elongating imaginal maxillæ. (γ) Those details which, once impressed by an imaginal structure, have remained after the latter has shrunk and changed. This includes the large pectinated antennæ of female pupæ, giving rise to imagines with filiform antennæ. (δ) Those details which have followed the collapse of the contained imaginal structure, but have kept behind the latter, so that they form actual proofs of the shrinkage by showing to us that the imaginal structures were once a size larger. This includes the wings of female pupæ without the power of flight in the imago stage.

III. The third head includes those structures or marks which are due to the adult larva, and are of no morphological significance. These are either a mere concession to the mechanical condition of the process of pupation (scars of claspers and processes) or are due to the larval pigment still lingering unchanged in the pupal hypodermis cells.

IV. The fourth head includes those features which are due to the exigencies of pupal life as it now is. Such are the protective forms, markings, and colours of exposed pupæ; the colour of those that pupate in or upon the earth; and the rings of locomotive hooks

or spines possessed by those that pupate in tubular galleries cut in plant-stems or formed by rolled-up leaves.

Conclusions as to the Nature of Lepidopterous Metamorphosis.—Many writers have pointed out that the form of metamorphosis which consists of three sharply separated stages has been, in all probability, derived from a form in which many closely similar stages gradually led up to the final sexually mature form. The present metamorphosis of Lepidoptera &c. has been derived from the more ancestral form, still witnessed in the Orthoptera, by the omission of intervening stages, and also by the subsequent specialization of the final stage. In estimating the position of the lost stages it is most important to gauge the morphological relation of the pupa to larva and imago. Directly we attempt this comparison we find that, whatever morphological feature we adopt as a criterion, the position of the pupa is immensely nearer to the imago than to the larva. The great morphological break is between larva and pupa, an interval so wide as to dwarf the minor differences between pupa and imago.

At the change of skin which separates the two former stages we suddenly pass from a stage with simple eyes, without wings or external generative organs, into a stage with compound eyes, wings, and well-marked external generative organs. We may therefore safely conclude that many stages have been lost between larva and pupa.

At the time when these stages intervened the stage represented by the pupa was very near to the final form, if not the final form itself. This conclusion follows from the close morphological similarity of pupa to imago, and from the presence of distinct external generative organs.

The suppression of intervening stages has left the first or larval stage in an extremely ancestral condition, so that the larva in Lepidoptera is far more ancient than the first stage of those insects (Orthoptera), which still retain the more ancestral method of metamorphosis. These, therefore, have lost the early stages, while Lepidoptera &c. have lost all the stages intervening between the earliest and a very late stage.

It is probable that there are very few, if any, lost stages between pupa and imago, but the differences between them are due to subsequent specialization in the latter. Such specialization is frequently of quite recent date.

It is most interesting to inquire for the possible reasons which determined the loss of the intervening stages and the concentration of metamorphosis. It is quite clear that the loss is associated with, and in fact rendered possible by, the quiescence of the pupal stage, during which the tissues can be broken down (histolysis) and re-developed in the form of the imago. Thus the great morphological interval between larva and imago can be crossed without the need of intervening stages.

One interesting result of pupal quiescence and of histolytic change is the conclusion that there is no definite pupal stage, as far as the internal parts are concerned. The external parts will be shown to possess a clear and obvious morphological meaning, but a meaning which only becomes clear on the supposition that the internal parts possessed an equally definite significance at some time in the past. The sculpture on the surface of the pupa—its parts and their arrangement—point to a very definite stage; but beneath the surface we find either a gradual transition from larval to imaginal organs or the

larval tissues in a state of histolysis, from which the imago will be rapidly built up at a later period.

Sir John Lubbock * has suggested that the explanation of the quiescent pupal stage is to be found in the difficulty with which a *gradual* transition could be effected from the biting mouth-parts of the larva to the sucking mouth-parts of the imago. The intermediate form of mouth would be unfitted for either biting or sucking successfully; hence the necessity for a quiescent stage in which no food is taken, and during which the change can be accomplished.

The principle which underlies Sir John Lubbock's suggestion has probably been of very great importance for other structures as well as the mouth-parts, viz. the fact that specialization to the conditions of life in the final sexual phase of existence is thus readily attained without interfering with the great specialization of other antecedent stages. It would be of the greatest importance for the imago to be able to modify the methods by which it is adapted to its environment, without the cumbrous necessity for such modifications to be gradually introduced through a number of previous stages. This is the explanation of the quiescent pupal period adopted by the late F. M. Balfour†. A general support to this argument is to be found in the fact that the differences between larva and imago are far less in the Orthoptera, with their gradually progressive metamorphosis. The difficulty of specialization to different conditions in different stages has here been met by uniformity in the stages, so that one form of specialization is, with slight differences, available throughout.

I will briefly recapitulate the history of metamorphosis, which is, I believe, supported by the facts to be described in this and succeeding papers. One of the terminal stages of a gradually progressive metamorphosis, sufficiently advanced to possess well-formed external reproductive organs, became quiescent; this stage is largely preserved in the external morphology of the pupa. Histolysis and re-development of the final form then occurred, gradually displacing the stages immediately antecedent to the quiescent phase, which previously had been necessary in order to lead up to the latter and the final form to which it gave rise. Becoming more and more complete, the changes beneath the surface of the pupa gradually displaced the earlier stages until only the first, the larval stage, remained. The morphological intervals between pupa and larva and between pupa and imago have been subsequently widened by specialization to the conditions peculiar to each stage. The comparatively slight differences between pupa and imago are entirely to be explained in this way; for very few, if any, stages have been omitted between them.

These conclusions apply to the Lepidoptera, and probably with slight modification to other orders with a similar form of metamorphosis.

PART I.—THE PERSISTENT TRACES OF LARVAL STRUCTURES UPON THE PUPA.

Before considering the number of abdominal segments and their relation to those of the larva, it is necessary to describe certain characters which will form very convenient

* 'Origin and Metamorphoses of Insects.'

† 'Comparative Embryology.'

aids in this part of the investigation. Not only is there the test of the spiracles, but owing to the manner in which the pupa is formed beneath the larval skin, almost any outgrowth of the surface of the latter leaves its impress upon the former. The scars thus produced are merely incidental and of no morphological significance, but they are extremely valuable as proofs of segmental identity. Other larval characters also appear on the surface of the pupa; their morphological meaning varies in the different cases.

1. *The Claspers.*—The posterior or anal pair of claspers are generally distinct in the pupa as convex cushion-like structures on each side of the anus. In certain individuals they may even retain the relative size and appearance which are characteristic of the larva (see Plate XX. figs. 8, 9, 10, showing different aspects of these parts in an extreme variety of *Smerinthus populi*). While the posterior claspers are thus represented by pupal structures and not merely by scars, the four anterior pairs only leave functionless traces upon the pupal cuticle. The first and second pairs are hidden beneath the fore wings, but on raising the latter (in pupæ placed in spirit immediately after throwing off the larval skin) the scars can be seen, and they may even be detected in living pupæ with exceptionally transparent wings (e. g. *Miselia oxyacanthæ*). The third and fourth pairs of claspers nearly always leave conspicuous scars upon the fifth and sixth abdominal segments (see Plate XXI. fig. 17 &c.).

2. *The Caudal Horn of Sphingidæ &c.*—This structure always leaves a scar on the pupa, even in those species in which it is feebly developed at the close of larval life (e. g. *Chærocampa elpenor* &c.). The scar is especially distinct in *Macroglossa stellatarum*. In most pupæ of Sphingidæ there is a well-marked depression on the eighth abdominal segment behind the scar left by the horn. This must be due to the bending downwards of the horn, which becomes quite horizontal before the larval skin is thrown off, so that the posterior edge of its base and the continuous adjacent larval cuticle are depressed and leave a permanent impress upon the yielding surface of the pupa. In *Smerinthus tiliæ* the general surface of the pupa is corrugated, but the scar of the horn is quite smooth. (See Plate XX. figs. 13 & 14 for the scar in this species, fig. 2 for an unusually prominent trace in *S. ocellatus*, fig. 4 for the normal scar, figs. 9 and 10 for the scar in *S. populi*.)

The blunt horn of *Endromis versicolor* also leaves a large scar, very different in appearance from the rest of the pupal surface (see Plate XXI. fig. 14 for an unusually conspicuous example).

Not only does a firm chitinous structure leave a distinct trace on the pupa, but soft elevations of the surface, like those seen upon the first and eighth abdominal segments of the larva of *Acronycta psi*, can be plainly detected upon the corresponding segments of the pupa (see woodcut 1, $\times 2$, in which the pupa is seen from its dorsal aspect).

3. *Other Larval Structures which can be detected on the Pupa.*—The peculiar rough plate upon the dorsal surface of the anal flap of the larva of *Smerinthus tiliæ* is represented by the extremely rough dorsal surface of the terminal spine of the pupa, and is thus a valuable aid to the identification of these two structures. In the larva of *Pygæa bucephala* there is a “glabrous corneous black plate occupying the (dorsal surface of the) anal flap” (Newman, ‘British Moths,’ 1869, p. 220). This is represented on the anterior

dorsal part of the tenth abdominal of the pupa, which forms a deep furrow with the ninth abdominal. The edge of the furrow is crenated (see Plate XXI. fig. 6).

4. *Larval tufts of Hairs indicated on the Pupa*.—In the larva of *Orgyia pudibunda* there is a well-known tuft of hairs, the “tussock,” upon each of the first four abdominal segments, and these are distinctly marked on the first three abdominal segments of the pupa, and perhaps to a slight extent on the fourth. On the other hand, there is a long pencil of hairs on the eighth abdominal segment of the larva, of which I could detect no trace in the pupa.

The larva of *Orgyia antiqua* also possesses four large tufts in the position described above, and the indication of these structures upon the first three abdominal segments is perhaps the most conspicuous feature of the pupa; but there is not the slightest trace of the fourth tuft. The three tufts in the pupa form squarish light-coloured patches, which are very distinct against the dark pupal cuticle, and are especially prominent and well defined in male pupæ, which are much blacker than females. The entire absence of any trace of the fourth tuft is very remarkable.

These appearances on the pupæ belong to a very different category from the merely mechanical scars, such as those produced by the caudal horn in *Sphingidæ* &c. and by

Fig. 1.

Fig. 2.

the four anterior claspers; for in the former case the pupa does not bear a scar of the larval tuft, but possesses a true hairy tuft itself. On the other hand, hairy prominences may be represented by mere scars, as in *Acronycta psi* (see woodcut 1).

Furthermore, in the pupa of *Saturnia carpini* distinct scars may be found which have been left by many of the brightly coloured hair-bearing warts of the larva. The scars are quite hairless and are much smoother than the rest of the pupa; they are rather depressed below the general surface.

5. *Larval Markings upon the Pupa*.—Sometimes the characteristic markings of the larva may be seen upon the pupa immediately after the skin of the former is thrown off, and these appearances may be fixed by placing the pupa in spirit and thus checking the darkening of the surface. The persistence of such colours depends upon the fact that the hypodermis cells of larva and pupa are the same; so that any pigment contained in them during larval life may remain unchanged after the pupal period has begun. Such colours are, of course, concealed in the living pupa by the opaque cuticle. I first noticed the persistence of larval colours in the freshly formed pupa of *Sphinx*

*ligustri** (see woodcut 2, natural size, showing the posterior part of an undarkened male pupa from the left side). The purple borders of the stripes are seen to bear a relation to the segments similar to that borne during the larval stage. This is especially well seen in the border of the last stripe. In the larva the last white stripe crosses the seventh abdominal and enters the base of the caudal horn on the eighth; its border is, of course, just in front of it during this course. The border in the pupa crosses the same segment, and its long axis points towards the anterior part of the scar of the caudal horn (see woodcut 2, *sc.*). So also the relation of the coloured borders to the spiracles is just the same as that of the larva. The borders in the figure are more distinct than in the spirit-specimen from which it was drawn, because the surface of the latter has darkened to some extent upon the back, and the borders appear to be merely lines of especial darkening as compared with the adjacent surface, which they resemble in colour (brown). In another spirit-specimen of *Sphinx ligustri* (preserved for nearly two years) the stripes remain very distinct and still retain a purplish tint. On removing a portion of the cuticle and examining its under surface, it was at once seen that the colour of the borders is due to pigment in the adherent hypodermis cells, which can be detached with loss of the colour. It is thus certain that the constitution of the coloured stripes in the pupa is similar to that in the larva, while the dark surface of the former is entirely different and due to a darkening of the cuticle.

Similar facts are true of the pupa of *Acherontia atropos*. When examined immediately after pupation the purple stripes and small circular patches (which probably spread from the bases of shagreen dots) of the larva are distinctly seen through the undarkened pupal cuticle. I have also observed the light oblique stripes, with their dark green borders, of *Smerinthus populi* and of *S. ocellatus*, conspicuously appearing upon the surface just after pupation.

The importance of these observations in homologizing the larval and pupal segments and structures is well shown by the following example:—"In the green freshly exposed pupa of *Agria tau* all the markings of the larva are very distinct, and the subspiracular line which forms so prominent a feature of the larva, and which is continued along each side of the anal flap to its extreme apex, is equally conspicuous in the pupa, and occupies an identical position in relation to the terminal anal spine, which in this species is blunt and covered with an immense number of irregular hook-like cuticular processes"† (see Plate XXI. fig. 16 for the general form of this part of the pupa). Hence the position of the marking affords valuable confirmation of the identification of the anal flap of the larva with the terminal spine of the pupa, to be further discussed below.

There is little doubt that the careful examination of freshly formed pupæ will prove that such markings are of very general occurrence.

* See Proc. Roy. Soc. vol. xxxviii. p. 278, in which this example is briefly described.

† Poulton, in Trans. Ent. Soc. Lond. 1888, p. 566.

PART II.—THE NUMBER OF ABDOMINAL SEGMENTS AND THEIR RELATION TO
THOSE OF THE LARVA.

It is obviously necessary to determine these points before proceeding to the consideration of the external organs of reproduction, for the segmental relations of the latter are of the highest importance.

1. *The Number of Abdominal Segments in the Larva.*—There is no difficulty about the seven anterior abdominal segments, each of which bears a spiracle. Behind the seventh, however, there is a somewhat confused mass of segments, bearing a single spiracle on its anterior part; this spiracle is usually larger than those upon the other abdominal segments (see woodcut 4). This confused mass is sometimes described as a single segment and sometimes as two. Careful comparison with the pupa proves that it is certainly made up of three segments.

Woodcut 3, $\times 2$, represents the posterior part of the larva of *Gonoptera libatrix*, as seen from the left side. The separation of the anterior, spiracle-bearing part of the mass of segments behind the seventh abdominal (VII) is extremely distinct in this larva, clearly forming the eighth abdominal segment (VIII). Behind this there is a small ninth abdominal (IX), which is clearly separated off dorsally, although less distinct ventrally.

The pairs of dorsal bristles shown upon the eighth and ninth abdominal segments in woodcut 3 are obviously homologous with those on the anterior abdominal segments. In woodcut 4, $\times 9$, the same parts are seen from the right side in the larva of a *Pyræ*, *Ephestia Kühniella*; the ninth abdominal is seen to be even more distinct than in woodcut 3, and to be clearly defined ventrally. In the larva of *Agria tau* the independence of the ninth abdominal (and the tenth also) is strongly confirmed by the resemblance of the pair of dorsal tubercles to those upon the anterior dorsal segments*. The accurate representation of these parts in many South-American larvæ should be studied in the plates of W. Müller's 'Südamerikanische Nymphalidenraupen' (Fischer, Jena, 1886).

In the pupa, this ninth abdominal segment, although small, is as distinct as any of the others; see, for instance, woodcut 5, $\times 7$, which represents the last three segments of a female pupa of *Pieris brassicæ*, seen from the left side: the same parts of the same pupa are seen from the dorsal aspect in woodcut 6, $\times 7$. The distinct independence of the ninth abdominal is shown with equal clearness in most of the figures on Plates XX. & XXI.

The part behind this segment in the larva forms a tenth abdominal. This segment is separated into a dorsal portion (x' in woodcuts 3 & 4), of which the posterior and lower part forms the anal flap, and a ventral portion (x), of which the anal claspers form the posterior and lower part; between the latter is the anus.

2. *The Relation of the Terminal Abdominal Segments of the Pupa to those of the Larva.*—The essential structure of the terminal parts of the vast majority of pupæ, as seen from the left side, is diagrammatically shown in woodcut 7. The identification of the various parts with those similarly numbered in the larva (woodcuts 3 & 4) is sufficiently obvious. The spiracle on the eighth abdominal is rudimentary in the pupa, although of exceptional

* See Poulton in Trans. Ent. Soc. London, 1888, p. 561; woodcut 4 is copied from plate xvii. fig. 9 accompanying that paper.

size in the larva. The identification of the terminal spine (x') with the anal flap of the larva was published by Mr. W. H. Jackson in 'Forms of Animal Life' (1888, p. 153). I also find from my notes that I had independently arrived at the same conclusion. Important confirmation is afforded by the previously-described relation of certain larval structures and colours to those of the pupa. When a spine is absent, and the terminal part of the pupa is rounded, the part above the anus nevertheless corresponds to the larval anal flap (see Plate XX. fig. 27, Plate XXI. fig. 12, &c.). The rounded cushion-like structure (x) represents the left anal clasper of the larva, and bears a similar relation to the anus and dorsal part (x'). The proof of this identification is chiefly found in the previously described exceptional individuals in which this part retains the characters of the anal claspers (see Plate XX. figs. 8, 9, 10).

An examination of Plates XX. and XXI. will show that the condition represented in woodcut 7 is typical among pupæ. There are, however, certain species in which the

arrangement is somewhat different. Woodcut 8 represents diagrammatically one of these exceptions. An example is found in the pupa of *Agria tau* (Plate XXI. fig. 16). The base of the terminal spine is somewhat constricted off from the rest of the tenth abdominal; the latter is divided into an upper and lower part by an oblique furrow. In certain *Geometræ* the same conditions are still more strongly marked; they are diagrammatically represented in woodcut 9. *Melanippe fluctuata* is a good example of this condition of the tenth abdominal (see Plate XXI. figs. 21, 22, 23), while *Amphidasis betularia* is transitional from this to the normal condition shown in woodcut 7 (see Plate XXI. fig. 20).

For a long time I believed that the tenth abdominal is in reality composed of two segments arranged, as in woodcut 7, one over the other. The arrangement shown in woodcut 9 is then explained by the supposition that the two component segments have assumed a more normal mode of succession, the anal segment (x in woodcut 7) becoming

the tenth, and separating the rostral segment (x' in woodcut 7) as the eleventh from any contact with the ninth. Now, however, I think it is far more probable that the line of separation between the two parts of the tenth abdominal in woodcut 7 merely corresponds to the posterior part of the chink beneath the larval anal flap. The constriction which in certain pupæ encircles the base of the terminal spine would then cease to have any morphological significance; and this is also rendered probable by the fact that closely allied pupæ are altogether without it. The existence of a distinct line separating the supposed anal segment into a ventral and dorsal part in the condition represented in woodcut 8, and the indication of such a division in the more pronounced condition represented in woodcut 9, are also irreconcilable with the view that the terminal spine of these woodcuts represents the whole of the dorsal part of the tenth abdominal (x' in woodcut 7).

We may therefore conclude that both larva and pupa possess ten abdominal segments; and even if this conclusion may require subsequent modification, the segmental relations of the external reproductive organs will be unaffected; for these structures only come into relation with the eighth, ninth, and the ventral (anal) part of the tenth abdominal segments.

PART III.—THE EXTERNAL GENERATIVE ORGANS.

1. *Introductory and Historical.*—It is very remarkable that these organs have not been universally recognized, considering that thousands of pupæ are examined every year by entomologists and dealers, while the organs are easily seen in large species by the naked eye. There are other well-known tests of the sex of pupæ, depending on the difference between male and female antennæ, and upon the greater size of the abdomen in the female. But the former only applies to certain species (in which such a difference exists), and in these the antennæ of the pupæ are far more alike in the two sexes than those of the imagines of the same species (as will be shown in a future paper). The latter test is even more precarious. I therefore think that a study of the sexual differences on Plates XX. & XXI. will be of practical assistance in many departments of the subject. I have myself found the knowledge invaluable for many years, in the management of some experiments with larvæ in which it was necessary to ascertain and allow for hereditary tendencies. The pupæ of moths can be arranged according to their sexes far more quickly than the imagines of the same species, except when there is some obvious secondary sexual character, such as a difference in the colouring of the wings, &c. The organs are especially easy to distinguish, because pupæ are either entirely hairless, and generally smooth in the region of these structures, or possess minute or scanty hairs which do not cause any obscurity.

In the first edition, now out of print, of 'Forms of Animal Life' (1870) by the late Professor Rolleston, these words occur on p. 76, in a description of the pupa of *Acherontia atropos*:—"The ninth abdominal ring is marked by a depression on either side of the middle ventral line, the lines limiting which extend into the interspace between it and

the eighth abdominal segment, and indicate thus the normal position of the outlet of the generative glands." It is very difficult to see how a morphologist could have come so near the discovery of the external organs of reproduction and yet have failed to find them. The only possible explanation can be that, in the examination from which the above description was written, only a single pupa was made use of, or perhaps a small number, all of which happened to be of the same sex. It is quite clear that Professor Rolleston was speaking of a female pupa, for the organs are so obvious as distinct structures in the males that they could not have been passed over. Besides, the description quoted above is under no circumstances applicable to the male sex, while it does form an imperfect account of the appearance in certain female pupæ.

On the other hand, almost all entomologists who have carefully figured large pupæ exhibit in their drawings traces of the sexual characters which are sometimes accurately rendered in the case of the males. Thus, Lyonet figures (plate 39. fig. 3) a pupa of *Cossus ligniperda* with distinct male organs; Moore ('Lepidoptera of Ceylon') represents some large pupæ with indications of the generative structures. Burmeister, in his beautiful illustrations of the Lepidoptera of the Argentine Republic, also represents these parts. Thus his plate 18. fig. 11 represents a distinct male pupa of *Attacus hesperus*; while his plate 20. fig. 5 B is an equally distinct female pupa of *Ceratocampa imperialis*. In the description of these figures the position of the generative aperture is pointed out, but the sexual differences are not observed. Mr. W. F. Kirby has pointed out to me that there is a brief description of the male characters in Berge's 'Schmetterlingsbuch' (5th ed. 1876, p. viii):—"Bei dem männlichen Geschlechte auf dem vorletzten Ringe zwei durch einen Eindruck getrennte Höckerchen."

The morphology of the sexual structures is never attempted in these descriptions, and the figures are not sufficiently accurate or detailed to be of any value. This is especially true of the female sex, and I believe that an accurate figure of the female characters has never been published until now.

I first noticed the male organs in a pupa of *Sphinx ligustri* in the autumn of 1883, and at once began to examine a number of pupæ in order to find the characters of the opposite sex. This led me to undertake a careful comparison of the external generative organs in a large number of species, and finally to investigate all the features which make up the external morphology of this stage in Lepidoptera. This investigation has been intermittently continued up to the present date. Many of the figures on Plates XX. and XXI. were drawn during the autumn and winter of 1883 and early in 1884, namely, Plate XX. figs. 3, 4, 5, 6, 7, 12, 13, 14, 16, 18, 19, 22, 30, 31, 32, Plate XXI. figs. 4, 5, 6, 7. When I showed these figures to Professor Moseley, who took a very great interest in the work, and helped me with many kind suggestions, and with the results of his own observations upon pupæ, he expressed the opinion that the figures should be made on a much larger scale. The size of the other figures on the two Plates was adopted as the result of this advice. The smaller figures are of the natural size, and are useful in showing how much can be made out with the naked eye.

I have also to thank my friends Professor Meldola and Mr. W. White for kindly providing me with much of the material which has been made the subject of investigation.

Mr. White spent a great deal of time and trouble in examining pupæ and putting aside the most favourable specimens for my use. I owe the specimens from which the following figures were made to his kind assistance:—Plate XX. fig. 26; Plate XXI. figs. 9, 12, 13, 24, 25, 30, 34. Plate XXI. figs. 1, 2, 28, and 29 were drawn from Professor Meldola's material. Figs. 1 and 2 represent two especially favourable individuals selected after the comparison of a very large number.

2. *The Male External Reproductive Organs.*—A casual examination of a large pupa with the naked eye, or of a small one with the assistance of a low magnifying-power, at once shows the existence of two convex or flattened, roundish, oval, or trianguloid tubercles, placed one on each side of the middle ventral line, in the ninth abdominal segment. Careful examination throws some doubt upon the certainty of this segmental relationship. There is no doubt, however, that the organs always occur *in the zone of the ninth abdominal*, viz. in an area which would be included in the segment if the boundaries of the latter were produced in the direction indicated by their course in the dorsal and lateral regions. Between the tubercles is a furrow which generally becomes a deep pit in its central part; this pit is the ancient opening of the pupal *vas deferens*, and it now corresponds externally to the termination of the ducts internally.

It is furthermore possible by carefully selecting the pupæ, to find individuals which approach the condition of a perforate orifice. I have found *Smerinthus populi* the best species for this purpose, and on examining the organs from the *inside* of the empty pupa-case of a favourable individual, the lips of the depression are seen completely introverted, their internal surface having the black appearance and peculiar roughened texture which is characteristic of the exterior of the pupa, and with which it is of course continuous. The surface of the introverted funnel-like opening is covered with the same lustrous white layer which invests the whole interior of the cuticle, and which therefore is contrasted very sharply with the internal surface or lumen of the funnel. In this case the funnel is not closed at its deepest point, the lumen being obstructed a little higher up by the fusion and hardening of the semifluid substance into a solid plug immediately after pupation. When looked at from within, the sides of the sharply truncated funnel are quite free, recalling most vividly the condition in which the lumen was perforate throughout. The whole appearance from within, in fact, singularly resembles that of one of the superficial functional spiracles looked at from the same point of view. These have similar introverted lips, also sharply truncated, and showing the characteristic black surface which lines the lumen. The rudimentary eighth abdominal spiracle, on the other hand, is completely closed below, and the white surface lining the pupal cuticle is unbroken over it. It is very remarkable that this most ancestral generative organ should in certain cases retain such strong indications of the time when it was functional.

On the other hand, there are proofs of the ancestral nature of the male organs, and of their rudimentary condition, as far as the pupa itself is concerned. Thus the individual differences are very great in position and form, and in the degree to which the structures are developed. Furthermore, these organs are often asymmetrical when all other parts of the pupa are entirely normal. The asymmetry may be slight, as in Plate XX. fig. 11,

or pronounced, as in Plate XXI. fig. 34, or accompanied by marked deformity, as in Plate XX. fig. 26.

I have already stated that these organs appear to the naked eye to belong to the ninth abdominal. They are represented in this position in all figures which are of the natural size. When moderate powers are employed, together with the best means of illumination, and when the most favourable individuals are selected for examination, the organs appear to be surrounded by a furrow or line which is continuous on either side with the boundary between the ninth and tenth abdominal segments. This interpretation is supported by Plate XX. figs. 17, 18, 19, 21, and 23, and Plate XXI. fig. 2; that is to say, it is supported by all the most carefully drawn and highly magnified figures. In some of these, and especially in Plate XXI. figs. 12, 13, the organs appear to belong to an anterior median extension of the tenth abdominal.

I have not described the differences between these organs in the various species examined, nor the sculpture of their surface as compared with that of the adjacent area, because all this can be sufficiently made out by studying Plates XX. and XXI., and by reading the description of the figures.

3. *The Female External Reproductive Organs.*—These organs will also be described briefly, and the reader is referred to Plates XX. and XXI. for the details of specific and individual differences.

When the female pupa is examined with the naked eye, or with a low magnifying-power, the first character which arrests attention is an anterior median ventral wedge-shaped extension of the tenth into the ninth and sometimes into the eighth abdominal segment. In the majority of pupæ this feature is certainly more conspicuous than the generative apertures, and I observed and figured it long before I had detected the latter. It is interesting to note that Lyonet figured it in the pupa of *Bombyx rubi*, although without any other feature characteristic of the external reproductive organs. (See Lyonet, plate xxiv. fig. 12.) The median prolongation is especially conspicuous in the pupæ of Heterocera, but distinct traces of it can be often made out in Rhopalocera. The anterior median ventral margin of the ninth abdominal is also prolonged into the eighth for a variable distance, thus permitting the ventral prolongation of the tenth abdominal, or the generative aperture in connexion with its apex, to extend beyond the zone of the ninth abdominal (see page 199). The development of both these median processes varies extremely, not only in different species but in different individuals of the same species. Sometimes there is a median line which traverses the prolongation of the tenth abdominal, as in *Macroglossa stellatarum* (Plate XX. figs. 24 & 25). Sometimes the base of the prolongation appears to be separated from the rest of the tenth abdominal as in *Cossus* and *Zeuzera* (Plate XX. figs. 27 and 29; Plate XXI. fig. 1.) Any discussion as to the possible meaning of this feature is better deferred until after the consideration of the generative apertures.

There are two distinct generative openings in female pupæ—an anterior for the *bursa copulatrix*, and a posterior for the oviducts. The anterior is probably always associated with the eighth abdominal; it is more distinct than the other, and is usually provided with prominent lips. It is often slit-like, and extends from the posterior to the ante-

rior boundary of the segment, but is especially dilated at its posterior end (see Plate XX. figs. 15, 27, & 29). In a single individual of *Orgyia antiqua* (Plate XXI. fig. 10) it appears to be placed on a forward extension of the ninth abdominal into the eighth, but in another individual of the same species its position is normal (Plate XXI. fig. 9). We may safely conclude that the anterior generative opening is associated with the eighth abdominal segment.

The segmental relation of the posterior generative opening is far more difficult to determine. The two views as to its relationship appear to be about equally supported by the figures on Plates XX. and XXI. These are illustrated by woodcuts 10 and 11. In the former the posterior aperture is placed on the ninth abdominal, immediately in front of, but distinct from, the apex of the median prolongation of the tenth abdominal.

In woodcut 11 the aperture is placed on the apex of the prolongation itself, and therefore belongs to the tenth abdominal segment. In the majority of pupæ the opening occurs at the apex, and may or may not be considered to belong to it. This is the case, for example, with figs. 25 and 29 on Plate XX. Whether connected with the apex or not,

the aperture is always placed close to it. The posterior generative opening is often obscure and unrecognizable on the surface (*e. g.* Plate XX. fig. 1), and is often fused with the anterior aperture (*e. g.* Plate XX. fig. 8). Even when the two openings are fused and are prolonged into a common invagination, the double nature of the latter is shown by a furrow (Plate XXI. fig. 19). The posterior opening may be surrounded by prominent lips or by a swollen margin (*e. g.* Plate XX. fig. 15; Plate XXI. fig. 15), or it may be without these features (Plate XXI. fig. 3).

Although the female organs are not asymmetrical like those of the male, they are subject to even greater individual differences.

The pupæ of *Rhopalocera* possess essentially similar openings, but they are much more difficult to interpret because of the specialization in shape and the amount of surface sculpture. The ventral area of the ninth abdominal may even be entirely hidden (*e. g.* the male *Nemeobius lucina*, Plate XXI. figs. 32 & 33). Figs. 24-31 on Plate XXI.,

selected from very favourable individuals, prove that both male and female external generative organs of Rhopalocera are essentially similar to those of the Heterocera.

A still more typical example is afforded by the pupa of *Pieris brassicae*, of which the male is shown in woodcut 12, $\times 7$, and the female, from two points of view, in woodcuts 13 and 14, $\times 7$.

The constancy and distinctness of the median prolongation of the tenth abdominal and the relation of its apex to one of the generative apertures indicates that it possesses some important morphological significance. Its shape suggests that it may represent an ancestral ovipositor formed as an anterior ventral extension of the tenth abdominal, and now fused to the pupa in its position of rest. Just as the male intromittent organ seems to be now only represented by the cuticle of that part of it which appeared on the surface when it was withdrawn, so the ancestral ovipositor is only represented by its external cuticular layer. The slight shifting of the generative opening, shown in woodcut 10, does not appear to disprove this hypothesis.

This hypothesis also explains the fact that there is a separate opening into the *bursa copulatrix*. Copulation would be almost impossible if the female aperture were placed on the apex of a conical process; hence the necessity for a more accessible aperture. This arrangement having been once set up, would be retained after the disappearance of the necessity under which it originally arose, because of the many co-adaptations which would have been entailed in both sexes.

DESCRIPTION OF PLATES XX. & XXI.

Representing the characters of the terminal abdominal segments and the external reproductive organs of Lepidopterous pupæ.

(The abdominal segments are indicated by Roman numerals, the anus by A, the terminal spine by Sp. Other structural features are described with reference to their segments, and will be identified easily.)

PLATE XX.

All the figures on this Plate represent the pupæ of Heterocera.

Figs. 1-7. The terminal abdominal segments of the pupa of *Smerinthus ocellatus*, showing the form of the external reproductive organs.

Fig. 1. $\times 7$. The last three abdominal segments of a female pupa, seen from the ventral aspect. These segments, being the 8th, 9th, and 10th abdominal, are indicated by the numbers VIII., IX., X. The number VIII. is placed close to the last spiracle, rudimentary in the pupa, although functional in the larva. The rough terminal spine (Sp.) forms the extremity of the pupa; immediately in front of it (in the ventral line) is the anus (A), which is very distinctly indicated. The boundary between the 9th and 10th segments is prolonged forwards in the ventral line,

and the apex of the narrow triangular area which is thus formed represents the opening of the oviducts, invisible in this and most individuals of the species, although sometimes seen. Immediately in front of the apex of the above-mentioned area is the second or anterior generative aperture, that of the *bursa copulatrix*. This is very distinctly marked and is bounded laterally by prominent convex lips; it thus resembles the form of the male generative opening, but can be readily distinguished in that it is placed in the 8th abdominal segment, while the male aperture is situated in the 9th.

- Fig. 2. $\times 7$. The same pupa as seen from the right side. The posterior part of the seventh abdominal segment is shown in addition to those represented in fig. 1. The number VIII. is placed close to the dorsal projection which corresponds to the caudal horn of the larva, and which is very exceptionally developed in this individual. Immediately below the terminal spine (Sp.) is seen a curved line dividing the tenth segment into an upper and a lower (or anal) part.
- Fig. 3. Natural size. The terminal part of a female pupa, as seen from the ventral aspect in a good light. The narrow pointed prolongation of the boundary between the ninth and tenth abdominal segments is distinctly seen, although neither of the generative openings were visible in this individual without magnification. The anus is distinct, and the cushions on each side of it (representing the anal claspers of the larva) are somewhat more prominent than usual.
- Fig. 4. Natural size. The same pupa as seen from the left side. Beneath the reference letter VIII. a normal trace of the larval caudal horn is seen, indicating the exceptional character of fig. 2 in this respect. The trace consists of an anterior slight elevation formed by the soft surface of the pupa rising in the hollow interior of the horn, and a posterior slight concavity caused by the hinder margin of the base being depressed into the soft surface when the horn is bent backwards, becoming nearly horizontal, before pupation.
- Fig. 5. Natural size. The terminal part of another female pupa, seen from the ventral aspect; the opening into the *bursa copulatrix*, with its lateral lips, is peculiarly distinct.
- Fig. 6. Natural size. The terminal part of a male pupa, seen from the ventral aspect. The opening of the male ducts is distinctly seen, placed between the prominent lips upon the ninth abdominal segment.
- Fig. 7. $\times 2$. The ventral part of the ninth abdominal segment of the last pupa, showing the external reproductive organs more distinctly. The small pit in front of the organ is merely an accidental irregularity of the surface.

Figs. 8-11. The Terminal Abdominal Segments of the Pupa of *Smerinthus populi*.

- Fig. 8. $\times 5.25$. The last three abdominal segments of a female pupa, seen from the ventral aspect. The anus is concealed in this position, owing to the altogether exceptional size of the anal cushions, which, in this individual, even retain the form of the larval claspers. An elongated opening, surrounded by a raised border, is situated in the normal position in front of the apex of the narrow median prolongation from the tenth abdominal segment. The opening is seen to be divided in two; it is probable that the posterior division represents the mouth of the oviducts; the anterior division, of course, corresponds to the *bursa copulatrix*. The remarkable sculpture of the surface is indicated in the figure.
- Fig. 9. $\times 5.25$. The same pupa, as seen from the left side; the scar of the caudal horn is distinct, and the remarkable size and shape of the left anal cushion is better seen than in the previous figure.
- Fig. 10. $\times 7$. The same pupa, as seen from the left side and behind. The object of the figure is to show the relative positions of terminal spine, anus, and anal cushions. These bear precisely the same relation to each other as the anal flap, anus, and anal claspers of the larva, thus

supporting other observations which prove that these parts are respectively homologous. The external reproductive organs are seen obliquely, and therefore indistinctly in this and the last figure.

- Fig. 11. $\times 4$. The last three abdominal segments of a male pupa, seen from the ventral aspect. The male opening is distinct on the ninth abdominal segment; its direction is somewhat oblique, an irregularity which is not uncommon and probably follows from the extremely ancestral character of the organs. The lateral lips are flattened and marked with a sculpture which is different from that of the surface of the ninth abdominal segment. The anal cushions are of normal size, and serve as a gauge of the amount of abnormality of figs. 8, 9, and 10 in this respect.

Figs. 12–14. The Terminal Abdominal Segments of the Pupa of *Smerinthus tilia*.

- Fig. 12. Natural size. The last four abdominal segments of a female pupa, seen from the ventral aspect. The median prolongation of the tenth abdominal is distinct, and the median slit in front of its apex represents one or both generative openings.
- Fig. 13. Natural size. The last five abdominal segments of a male pupa, seen from the left side. The scar of the caudal horn is distinctly seen in profile. The generative organs cannot be seen, but the contour of the ventral part of the terminal segments is characteristic of the male sex.
- Fig. 14. Natural size. The last three segments of a pupa (sex unnoted), seen from the dorsal aspect, in order to show the scar of the caudal horn from above.

Figs. 15–19. The Terminal Abdominal Segments of the Pupa of *Acherontia atropos*.

- Fig. 15. $\times 9$. The median ventral part of the last three segments of a female pupa. Both generative openings are distinctly visible in this individual; the opening of the oviducts is large and surrounded by a thickened V-shaped lip. It is placed in front of the apex of the median prolongation from the tenth abdominal, and appears to be clearly situated in an anterior median extension of the ninth abdominal segment. The opening into the *bursa copulatrix* is immediately in front of the other aperture, but separated from it by the boundary between the eighth and ninth abdominal segments. The opening extends forward as a narrow median slit as far as the anterior boundary of the eighth abdominal. The anus (A) is distinct on the tenth abdominal. The sculpture on the surface of the pupa and the various wrinkles &c. are carefully copied in the figure. These details required for their elucidation the most careful examination of an especially favourable individual in a very strong light. The general resemblance of the generative apertures to those of a well-marked individual of *Cossus ligniperda* is very striking (compare figs. 27 and 29).
- Fig. 16. Natural size. The last three segments of a female pupa, seen from the ventral aspect. The generative apertures could not be made out without magnification, but the median prolongation was very distinct, far more so than in the last figure. In front of the anus (A), at the base of the median prolongation, there is the deceptive appearance of an opening with lips, due to wrinkles in the pupal case. The true generative openings never assume so posterior a position. In fig. 15 the true nature of the marking is apparent.
- Fig. 17. $\times 9$. The median ventral area of the ninth and the anterior part of the tenth abdominal segments of a male pupa. The figure hardly needs description as the male organs are quite typical. The lateral tubercles are roundish and somewhat flattened. The sculpture of the surface is represented. The exact relation of the male organ to the boundary between the ninth and tenth abdominal segments varies greatly in different species (compare figs. 11, 20, 21, 23).

- Fig. 18. Natural size. The last three segments of a male pupa, seen from the ventral aspect, showing the appearance of the male organ when looked at without magnification.
- Fig. 19. $\times 2$. The median ventral area of the ninth and the anterior part of the tenth abdominal segments of the pupa represented in the last figure, showing the form of the male organs with greater distinctness. The three minute pits in front of the reproductive organ are probably merely an accidental conformation of the cuticle, for they are not found in other individuals (compare fig. 17).

Figs. 20, 21. The Terminal Abdominal Segments of the Pupa of *Sphinx ligustri*.

- Fig. 20. $\times 4$. The ninth and tenth abdominal segments of a male pupa, seen from the ventral aspect, showing the sculpture of the surface and the male reproductive organ. The latter is typical; its relation to the boundary between the ninth and tenth abdominal segments is better shown in the next figure, where it is seen to be nearly the same as in *Acherontia atropos* (fig. 17).
- Fig. 21. $\times 26$. The median ventral area of the ninth and adjacent parts of the eighth and tenth abdominal segments, showing the male organ and the surface sculpture very distinctly; the lateral tubercles are more closely applied than in *Acherontia atropos*. The pit in front of the reproductive organ is merely an individual peculiarity.

Figs. 22, 23. The Terminal Abdominal Segments of the Pupa of *Deilephila euphorbiae*.

- Fig. 22. Natural size. The last three segments of a male pupa, seen from the right side. The rudimentary spiracle and the scar of the caudal horn are seen on the eighth abdominal. The horizontal furrow which divides the tenth abdominal into a dorsal (rostral) and ventral (anal) part is unusually distinct. The division is rendered especially apparent because the dorsal part extends further anteriorly than the ventral, so that the ninth abdominal is narrow in front of the former and becomes suddenly broader in front of the latter.
- Fig. 23. $\times 26$. The median ventral area of the ninth and adjacent parts of the eighth and tenth abdominal segments, showing the male organ and the sculpture of the surface very distinctly. The male organ is somewhat asymmetrical. The two tubercles in front of it are probably an individual peculiarity.

Figs. 24, 25. The Terminal Abdominal Segments of the Pupa of *Macroglossa stellatarum*.

- Fig. 24. $\times 4$. The last four segments of a female pupa, seen from the ventral aspect. The functional spiracles on the seventh abdominal and the rudimentary spiracles on the eighth are represented in profile. The posterior part of the pupa gradually tapers into the sharp black rostrum. The anus (A) is distinct. The chief peculiarity of the pupa is the remarkable distinctness of both the female reproductive apertures. Although clearly seen in this figure, their relation to the segments is better studied in the more highly magnified fig. 25.
- Fig. 25. $\times 40$. The median ventral area of the last three segments of the pupa represented in the preceding figure. Of the very distinct reproductive openings, the anterior, leading into the *bursa copulatrix*, is seen to belong to the eighth abdominal, while the posterior, opening into the oviducts, apparently belongs to the ninth abdominal. The ventral prolongation of the boundary between the ninth and tenth abdominal is marked by a narrow pointed median band prolonged from the area round the anus (A). The latter is very distinct. The surface of the pupa is everywhere marked by circles with a dot in the centre of each, representing the (bristle-bearing) shagreen tubercles of the larva. The figure was drawn from a transparent object.

Fig. 26. The Terminal Abdominal Segments of the Pupa of *Sesia fuciformis*.

Fig. 26. $\times 14.5$. The last two segments of a male pupa, seen from the ventral aspect. The object of the figure is to show the remarkable distortion of the male organs in the individual represented. This is not accompanied by any want of symmetry in the adjacent parts. The anus (A), the large rostrum, the form of the segments, except in the parts directly affected by their close proximity to the male organs, are all undistorted.

Figs. 27-32. The Terminal Abdominal Segments of the Pupa of *Cossus ligniperda*.

Fig. 27. $\times 7$. The last three segments of a female pupa, seen from below, behind, and the left side. The reproductive organs were especially distinct in the individual figured. On the eighth abdominal the rudimentary spiracle and part of the dorsal semicircle of hooks are seen, together with the opening into the *bursa copulatrix*, which consists of a main aperture close to the posterior boundary of the segment and a narrow slit-like forward extension which reaches the anterior boundary. The semicircle of hooks on the ninth abdominal is also seen, together with the distinct opening into the oviducts, normally placed at the apex of the median prolongation of the tenth abdominal. On the tenth abdominal the anus is seen at A; the segment is divided, as in other pupæ, into a ventral (x) and a dorsal (x') part. The semicircle of hooks on other adjacent abdominal segments is imperfectly represented on the tenth abdominal. In the median ventral line between the anus and the anterior prolongation there is a mark like that in a corresponding position on the female pupa of *Acherontia atropos* (fig. 16). In both pupæ the mark is due to wrinkles in the pupa-case, and is probably of no morphological significance.

Fig. 28. $\times 50$. The median ventral area of the eighth, ninth, and part of the median prolongation from the tenth abdominal segments of the same pupa, as seen from within, from the right side and above. The main opening of the *bursa copulatrix* is seen to be prolonged into a laterally compressed funnel-shaped invagination of the cuticle, while the anterior extension is also distinctly marked by a long narrow ridge on the inner surface of the eighth abdominal. The opening of the oviducts is also marked by a very distinct invagination continuous posteriorly with the ridge-like boundaries of the median prolongation of the tenth abdominal. The small hemispherical elevation immediately in front of the last-named invagination is probably an individual variation.

Fig. 29. $\times 9$. The median ventral area of the eighth, ninth, and tenth segments of the same pupa, as seen from the ventral aspect. Many of the appearances described in fig. 27 can be followed more accurately and in greater detail. The surface sculpture is carefully figured. The above-described mark in front of the anus (A) is clearly shown, together with a pit in the posterior part of the seventh abdominal. The latter structure is probably also devoid of morphological significance.

Fig. 30. $\times 4$. The last two segments of a male pupa, seen from below and behind. The anus (A) is distinctly seen as a vertical slit in the ventral part of the small tenth abdominal. The spines which represent the semicircle of hooks on other adjacent abdominal segments are far less numerous than in the same part of the pupa shown in fig. 27, but, as in the latter, a single spine placed on each side of the anus is especially strong. The external reproductive organ is distinctly seen on the ninth abdominal; the lateral tubercles are flattened. Anterior to the organ there is a small flattened area with a different appearance from the rest of the surface. The semicircle of hooks on the ninth abdominal is seen, except in its dorsal part, which in this position is concealed by the tenth abdominal.

Fig. 31. $\times 2$. The last three segments of the same pupa, as seen from behind. The semicircles of hooks

are distinct on the eighth and ninth abdominal segments. The rudimentary spiracle on the former and the male organs on the latter are also seen. The division of the tenth abdominal into a ventral (anal) and dorsal part is distinctly shown. Four small spines are placed on the latter part, as in fig. 27.

- Fig. 32. Natural size. The last five segments of the same pupa, as seen from the right side. The semi-circles of hooks on the sixth, seventh, eighth, and ninth abdominal segments are distinctly seen, together with the functional spiracles on the first two of these and the rudimentary spiracle upon the eighth abdominal. Some slight irregularities of the surface below the spiracle on the sixth abdominal represent the larval clasper. The two parts of the tenth abdominal and its imperfect semicircle of spines are also seen, together with the male organs on the ninth abdominal.

PLATE XXI.

Figs. 1-23 represent Pupæ of Heterocera; the remaining figures represent the Pupæ of Rhopalocera.

Figs. 1, 2. The Terminal Abdominal Segments of the Pupa of *Zeuzera æsculi*.

- Fig. 1. $\times 26$. The median ventral area of the eighth, ninth, and the anterior part of the tenth abdominal segment of a female pupa. The resemblance to the pupa of *Cossus* is very marked (compare Plate XX. fig. 29), although the two reproductive openings are almost fused together. The surface-sculpture is represented. The anterior prolongation of the tenth abdominal is very distinct, as in *Cossus*, although in both these species its base is separated from the rest of the segment by a well-marked line of demarcation and by a difference in the character of the surface.
- Fig. 2. $\times 26$. The median ventral area of the ninth and the anterior part of the tenth abdominal segment of a male pupa. The male organ is beautifully regular; the lateral tubercles are somewhat flattened. The relation of the organ to the division between the ninth and tenth segments is carefully figured.

Figs. 3-6. The Terminal Abdominal Segments of the Pupa of *Pygæra bucephala*.

- Fig. 3. $\times 5.25$. The last three segments of a female pupa seen from the ventral aspect. The median prolongation of the tenth abdominal is unusually long, so that its apex and the inconspicuous opening of the oviducts is carried forward beyond the middle of the eighth abdominal: the opening of the *bursa copulatrix* is distinct and has a thickened border. The anus (A) is small. The shape of the double terminal spine is remarkable. The rudimentary spiracles are seen at the sides of the eighth abdominal. The surface-sculpture is represented.
- Fig. 4. Natural size. A representation of the same parts (except that the seventh abdominal is also included) in another female pupa. The object of the figure is to prove that sexual characters are easily distinguished by the naked eye. A characteristic feature is afforded by the median prolongation of the tenth abdominal. The female sexual openings are only distinctly seen in the majority of individuals by means of a lens.
- Fig. 5. Natural size. The ninth, tenth, and the posterior part of the eighth abdominal segments of a male pupa, seen from the ventral aspect. The male organs are seen to be distinctly recognizable without magnification. They are characteristic in form and position.
- Fig. 6. Natural size. The same segments, as seen from the dorsal aspect. The object of the figure is to show a structure which corresponds to the black plate upon the dorsal surface of the larval anal flap. It is placed on the anterior dorsal margin of the tenth abdominal, and is valuable in homologizing the larval and pupal segments.

Figs. 7, 8. The Terminal Abdominal Segments of the Pupa of *Cerura vinula*.

- Fig. 7. Natural size. The last four segments of a female pupa seen from the ventral and posterior aspects. The median prolongation of the tenth abdominal is very distinct. A dorsal semicircle of spines is seen on the ninth abdominal, together with the indications of a semicircle upon the dorsal division of the tenth abdominal.
- Fig. 8. $\times 4$. The median ventral area of the ninth and adjacent part of the tenth abdominal segments of a male pupa. The male organs are characteristic in position and in form, except that the lateral tubercles are flattened as in *Cossus* (Plate XX. fig. 30).

Figs. 9, 10. The Terminal Abdominal Segments of the Pupa of *Orgyia antiqua*.

- Fig. 9. $\times 9$. The median ventral area of the eighth, ninth, and the anterior part of the tenth abdominal segments of a female pupa. The two closely adjacent generative openings are enclosed between lateral lips which bear a striking resemblance to each other. The posterior opening is in a normal position at the apex of the median prolongation.
- Fig. 10. $\times 9$. The same parts of another female pupa. A comparison between this and fig. 9 illustrates the very great amount of individual variation in the characters of the external reproductive organs. The differences, are, however, somewhat exaggerated by the fact that this figure was drawn from a transparent object, while fig. 9 was drawn from an opaque object. The two openings are seen to be fused. The posterior appears to belong to the tip of the median prolongation of the tenth abdominal, the anterior to a forward extension of the ninth; the latter is an exceptional appearance.

Figs. 11–13. The Terminal Abdominal Segments of the Pupa of *Odonestis potatoaria*.

- Fig. 11. $\times 5.25$. The last three segments of a female pupa seen from a ventral and posterior aspect. The anterior generative opening is very distinct and surrounded by lips; it is placed on the posterior part of the eighth abdominal. The posterior opening is probably represented by the median line immediately behind the anterior opening, but there is another mark placed more posteriorly, which may indicate its presence. The posterior end of the pupa is seen to be rounded.
- Fig. 12. $\times 7.5$. The last three segments of a male pupa, seen from a ventral and posterior aspect, but more posteriorly than in the last figure. Hence the division of the tenth abdominal into a ventral or anal (x) and dorsal (x') part is clearly indicated. The latter is entirely without a terminal spine, but is covered dorsally by minute hooks. The male organ is better studied in the next figure. The anus (A) is nearly terminal.
- Fig. 13. $\times 50$. The median ventral area of the ninth and anterior part of the tenth abdominal segments of the same pupa, showing the male organ and its relation to the segments. The surface-sculpture is indicated. The male organ is seen to be somewhat asymmetrical; it is surrounded by a thickened margin rather than by the two lateral lips which are distinct in most male pupæ (compare fig. 2). The relation to the limits of the ninth and tenth segments is carefully figured.

Fig. 14. The Terminal Abdominal Segments of the Pupa of *Endromis versicolor*.

- Fig. 14. $\times 7$. The last three segments seen from the dorsal aspect. The surface of the pupa is extremely rough and richly beset with spines, which take a backward direction, and probably assist in emergence from the cocoon. The scar of the caudal horn is unusually distinct and large in this individual; it is placed, as in the pupa of *Sphingidæ*, upon the eighth abdominal.

Figs. 15, 16. The Terminal Abdominal Segments of the Pupa of *Aglia tau*.

- Fig. 15. $\times 7$. The last three segments of a female pupa, seen from the ventral aspect. The surface-sculpture is represented. The generative openings are unusually distinct and separate from each other. The anterior (*bursa copulatrix*) occupies the entire breadth of the eighth abdominal; its margin is very prominent, and much resembles the appearance of the male organ. The posterior opening (oviducts) similarly occupies the entire breadth of the ninth abdominal; its margin is not so distinct as that of the anterior opening. The median prolongation of the tenth abdominal is short and broad. The anus (A) is placed on an oval convex area. Behind this area the base of the terminal spine is separated from the anal part of the tenth abdominal by a distinct furrow. The spine is rough and bristles with irregularly twisted thread-like processes. Its ventral surface, seen in the figure, is characterized by a large oval concavity marked by concentric lines.
- Fig. 16. $\times 7$. The last four segments of a female pupa, seen from the right side. The functional spiracle on the seventh abdominal differs from the rudimentary one upon the eighth in its oblique position. All the visible functional spiracles are oblique like that shown in the figure. The first thoracic is the only concealed spiracle in the pupa, for even the prothoracic is clearly exposed to view. The tenth abdominal is distinctly divided into a dorsal (x') and ventral part (x). The terminal spine (Sp.) is not, however, uninterruptedly continuous with the dorsal part, but is separated from the latter by a furrow which extends dorsally from that which was shown in the last figure, and surrounds the base of the spine. This tendency towards the separation of the terminal spine from the tenth abdominal is carried further in certain *Geometrae*.

Figs. 17-19. The Terminal Abdominal Segments of the Pupa of *Uropteryx sambucata*.

- Fig. 17. $\times 2$. The last five segments of a female pupa, seen from the ventral aspect. The traces of larval claspers are distinct upon the sixth abdominal. The morphology of the ventral area of the last three segments is confused by dark markings, and is better studied in the next figure.
- Fig. 18. $\times 9$. The last three segments of the same pupa, seen from the ventral aspect. The two generative openings are fused externally (compare the next figure), but the boundary between the eighth and ninth abdominal corresponds to the division between them. The base of the median prolongation from the tenth abdominal is marked by a triangular patch of dark pigment. The anus (A) is distinct; the terminal spines somewhat resemble those of *Melanippe fluctuata* (compare fig. 21).
- Fig. 19. $\times 50$. The ventral area of the ninth and adjacent parts of the eighth and tenth abdominal segments of the same pupa, as seen from within, from above, and the left side. The fused generative openings are seen to be invaginated to a considerable depth in the form of a long compressed ridge. The ridge is distinctly divided by a furrow continuous with the boundary between the eighth and ninth abdominal, indicating its essentially double nature. The relation of the posterior part of the ridge (the part which receives the oviducts) to the boundary between the ninth and tenth abdominal and to the median line along the latter seems to support the opinion that the posterior generative opening is associated with the median prolongation of the tenth abdominal.

Fig. 20. The Terminal Abdominal Segments of the Pupa of *Amphidasis betularia*.

- Fig. 20. $\times 5.25$. The last seven segments of a male pupa, seen from the right side. The dark bands on the posterior part of the fourth, fifth, and sixth abdominals indicate a peculiar texture

associated with the fact that motion is possible only at these intersegmental junctions. The rudimentary spiracle on the eighth abdominal forms a great contrast with those on the anterior segments. The junction of the terminal spine with the tenth abdominal is marked by a line. An oblique furrow extending posteriorly into the tenth abdominal probably represents an incomplete division into a dorsal and ventral part.

Figs. 21-23. The Terminal Abdominal Segments of the Pupa of *Melanippe fluctuata*.

- Fig. 21. $\times 26$. The last four segments of a female pupa seen from the ventral aspect. The boundaries of the median prolongation of the tenth abdominal are indistinctly visible and disappear towards the apex. This is a result of the polished surface of the pupa. Towards the posterior boundary of the eighth abdominal, the two generative openings are distinctly visible and are almost fused. It is impossible to feel any certainty as to the segments to which they belong, in this species. The anus (A) is very distinct and situated on a raised oval area. The terminal spine (Sp.) is distinctly segmented off from the tenth abdominal; it bears four bristles, the two central ones being stouter and larger than the others.
- Fig. 22. $\times 14.5$. The last four segments of another pupa (sex unnoted), seen from the dorsal aspect. The separation of the base of the spine from the tenth abdominal is very distinct. The median dorsal part of the anterior margin of the latter segment is extremely irregular.
- Fig. 23. $\times 26$. The last four segments of the female pupa represented in fig. 21, as seen from the right side. The furrow at the base of the terminal spine is very distinct. There is an oblique furrow extending posteriorly from the anterior margin of the tenth abdominal, as in the pupa of *Amphidasis betularia* (compare fig. 20).

The remaining Pupæ figured on Plate XXI. are those of Rhopalocera.

Figs. 24, 25. The Terminal Abdominal Segments of the Pupa of *Papilio podalirius*.

- Fig. 24. $\times 7$. The last three segments of a female pupa, seen from the ventral aspect. In this and the next pupa the surface-sculpture has been carefully figured. The opening of the *bursa copulatrix* is distinct on the eighth abdominal; there is a distinct median prolongation from the tenth abdominal, and the posterior generative opening is probably represented by the median line along its anterior part. The anus (A) is distinct, and there is a flattened area in front of it which terminates anteriorly in a raised rounded border overhanging the median prolongation of the tenth abdominal, and forming a very characteristic appearance.
- Fig. 25. $\times 7$. The same parts in a male pupa, seen from the same direction. The male organs are distinct and characteristic in form and position.

Figs. 26, 27. The Terminal Abdominal Segments of the Pupa of *Papilio machaon*.

- Fig. 26. $\times 7$. The last three segments of a female pupa, seen from the ventral aspect. The generative openings resemble those of *Papilio podalirius* (fig. 24). The position of the posterior opening on the median prolongation of the tenth abdominal is more distinct than in the latter pupa. The raised border in front of the anus (A) exhibits a tendency towards division into two parts. The part of the pupa represented in the figure is somewhat asymmetrical.
- Fig. 27. $\times 9$. The median ventral area of the ninth and adjacent parts of the eighth and tenth abdominal segments of a male pupa, seen from the ventral aspect. The male organs are distinct and characteristic. The raised border overhanging the male organs is not divided so deeply as that represented in the last figure.

Figs. 28, 29. The Terminal Abdominal Segments of the Pupa of *Ornithoptera minos*.

- Fig. 28. $\times 4.25$. The last four segments of a female pupa, seen from the ventral aspect. The anterior generative opening is distinct upon the eighth, and the posterior upon the ninth abdominal segments. Markings which can be easily distinguished from the surface-sculpture form the distinct boundaries of lips, as in the anterior opening of *Papilio* (compare figs. 24 and 26). The raised border overhanging the ninth abdominal is very broad, but strongly resembles that of *Papilio*. The close affinity between *Ornithoptera* and *Papilio* is proved by such resemblances between the pupæ. The terminal attachment is seen to be far stronger in the former, being related to the greater size and weight of the pupa.
- Fig. 29. $\times 4.25$. The same parts of the same pupa, as seen from the right side. The rudimentary spiracle upon the eighth abdominal is seen to be much smaller than the functional one upon the seventh. The tenth abdominal is clearly divided into a dorsal and ventral (anal) part. An immensely strong cable of black silk hangs from the hooks beneath the posterior extremity of the former, while the anterior extremity of the latter is formed by the raised border overhanging the ninth abdominal.

Fig. 30. The Terminal Abdominal Segments of the Pupa of *Gonepteryx rhamni*.

- Fig. 30. $\times 9$. The last three segments of a female pupa, seen from the ventral aspect. The anterior generative opening is large and distinct, occupying the whole breadth of the eighth abdominal. The outline of the large lateral lips is V-shaped. The posterior opening seems to be placed in the apex of the median prolongation of the tenth abdominal, while the ventral part of the ninth abdominal does not appear upon the surface of the pupa. In this respect the pupa resembles *Papilio* (compare figs. 24 and 26). The anus (A) is small but distinct; the area around and in front of it terminates anteriorly in a median and two lateral processes, the latter being spine-like. The hooks for attachment are placed upon a curved area below the posterior end of the pupa.

Figs. 31-33. The Terminal Abdominal Segments of the Pupa of *Nemeobius lucina*.

- Fig. 31. $\times 9$. The ninth and tenth abdominal segments of a female pupa, together with the median ventral area of the sixth, seventh, and eighth abdominal segments, seen from the ventral and posterior directions. The hairs on the surface of the pupa are not represented in the figure. The anterior generative opening is distinct; it is in the form of a slit occupying the median ventral line of the eighth abdominal. The posterior opening could not be identified, and only a very small part of the ventral area of the ninth abdominal could be seen on the surface, owing to the extension forward of the raised border, forming the anterior part of the tenth abdominal. The anus (A) is distinct, and the tenth abdominal is clearly divided into a dorsal (x') and ventral (anal) part (x).
- Fig. 32. $\times 9$. The last five segments of a male pupa, seen from the ventral aspect. The hairs are represented, but they should be of rather greater proportionate length. The scars of larval claspers are seen on the sixth abdominal. The anterior border of the tenth abdominal completely conceals the ventral part of the ninth, so that the male organs cannot be seen upon the surface.
- Fig. 33. $\times 26$. The last three segments of a male pupa seen from behind and the right side. The hairs are not represented. The manner in which the ventral part of the ninth abdominal segment is overlapped by the tenth is clearly shown. The dorsal (rostral) part of the tenth abdominal (x') is separated into three subdivisions by furrows. The rudimentary spiracle is distinct on

the eighth abdominal. The raised anterior border of the ventral (anal) part of the tenth abdominal (x) is very like that of *Papilio* and *Ornithoptera*, and exhibits traces of median division as in certain species of these genera (compare figs. 26 and 27).

The interpretation of the appearances in this species (*N. lucina*) presented great difficulty, but I believe that the solution suggested in figs. 31-33 is correct.

Fig. 34. The Terminal Abdominal Segments of some Rhopaloceros Pupa, probably that of *Arge galathea*.

Fig. 34. $\times 14.5$. The median ventral area of the last three segments of a male pupa. The anus (A) is distinct. The male organ is typical in form and position, except that it is twisted into an oblique direction. The object of the figure is to show the lack of symmetry in this structure in a pupa which was otherwise well formed. The uncertainty as to the species represented is therefore of comparatively small importance.

EXTERNAL REPRODUCTIVE ORGANS OF LEPIDOPTEROUS PUPÆ.