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THE EXTERNAL MORPHOLOGY OF THE LEPIDOPTEROUS PUPA: ITS RELATION TO THAT OF THE OTHER STAGES AND TO THE ORIGIN AND HISTORY OF METAMORPHOSIS.—Parts IV.-V.

BY

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VII. *The External Morphology of the Lepidopterous Pupa: its Relation to that of the other Stages and to the Origin and History of Metamorphosis.*—Parts IV. & V.

By Edward B. Poulton, *M.A., F.R.S., F.L.S., of Keble and Jesus Colleges, Oxford.*

(Plates XXVI. & XXVII.)

Read 20th March, 1890.

Contents.

Part IV.—The Pupal Antennæ.

1. *The Relation of Pupal to Imaginal Antennæ.*—When investigating the external morphology of the Lepidopterous pupa I had the great benefit of Professor Moseley's kind help and advice. Very early in the investigation he told me of some important observations he had made in 1871 upon the relation between the imaginal and pupal antennæ of *Saturnia carpini*. Corresponding with him on the subject, I received a letter, which is printed in full below. Apart from its great scientific value, the letter is of interest as showing the ready help and sympathy its writer was so pleased to extend to any scientific worker.

"14 St. Giles', Oxford,
January 1884.

"Dear Poulton,—I am very glad to hear of the continued success of your researches, and congratulate you on the matter. There is no need why anything should be said about my unpublished observations on the pupæ. I cannot lay my hand even on my drawing now. If, however, you think fit, you might mention that on your informing me of the line of work you had in hand I told you that I had observed that in *Saturnia carpini* the sheaths of the antennæ in the female pupa are large and inflated, with traces of pectination, resembling in this respect those of the male pupa, but in a reduced degree, although the antennæ of the female imago are, as well known, merely filiform. I concluded from this fact that in the ancestral *Saturniidæ* the imagos of both sexes must have had large pectinated antennæ, and that they had not been developed as such only in the male for sexual purposes, but must have been retained in the male and degenerated in the female. Further, it seemed to me that in the form of the pupa of Lepidoptera, and probably in Coleoptera and other forms also, many facts of important ancestral significance might be found preserved. The integument of the pupa, requiring for purposes of protection to be hard and rigid, when once it had assumed a particular shape suited to the contours of the body of the original ancestral insect, would retain that form indefinitely, although the shape of the several parts of the imago formed within it might, by the action of natural selection on it when in the free moving condition, alter considerably. It appears to be of no detriment to the development of the legs and the antennæ of the imago that their pupa-cases are far too big and do not fit. I concluded from the observations on *Saturnia* that probably members of the *Saturniidæ* must exist with well-marked pectinated antennæ in both sexes. I did not in the least know that such was the case, but soon saw that it is so on looking at Westwood's drawers of insects. If you think well to refer briefly to any of the above I shall be much obliged. It was in 1871 that I began to look into the matter, but it was cut short by my expedition to Ceylon. Wishing you all success, "I remain, &c.,

"H. N. MOSELEY."

Other parts of this paper, in addition to the section upon antennæ, bear witness to the general applicability of Professor Moseley's conclusions to the systems of organs which can be traced in the external morphology of Lepidopterous pupæ. At the same time it will be shown that the shrinkage of a part in the imago ultimately leads to the shrinkage of the corresponding part in the pupa. The latter change, however, keeps behind the stage of degeneration reached by the imago, so that an earlier condition of the imaginal organs can often be traced upon the pupa.

Directly my attention was called to the point I looked out for similar facts in many species of pupæ, and always with the same results. When there is much difference between the antennæ of male and female moths, there is always less difference between the antennæ of the sexes of their respective pupæ. I found this to be the case with pupæ of the genus *Smerinthus*, where the difference between the imaginal antennæ is not excessive, and in pupæ such as *Pygæra bucephala*, *Cerura vinula*, and *Orgyia antiqua*, in which the difference is much greater. In all cases we have evidence for comparatively recent increase of the sexual differences in the imago state.

A comparison of figs. 1, 2, 3, and 4 on Plate XXVI. will show the evidence upon which Professor Moseley relied for his conclusions. But the same conclusions are further supported by a more minute examination of the antennæ of the female imago. If these have undergone comparatively recent degeneration, we should expect to find great individual difference in the degree to which degeneration is carried, and we should expect to find traces of structures which were necessary for former functional activity. Figures 5 and 6 (Plate XXVI.) prove that the degree of degeneration varies greatly in different individuals (see description of figures), and that rudimentary sensory hairs are scattered over the reduced equivalents of the highly-developed rami of the male organ.

Corresponding facts come out still more clearly in the European *Aglia tau*, in which the imaginal sexual differences are even more strongly marked. There is an immense difference between the imaginal antennæ (compare figs. 9 and 10), while the corresponding pupal organs are not widely different (compare figs. 7 and 8). Although the antennæ of the female imago are extremely degenerate, a careful examination reveals traces of the structure which is so elaborately developed in the male (compare fig. 13 with figs. 11 and 12).

Orgyia antiqua affords an interesting comparison with *Saturnia* and *Aglia*, in that the antennæ of the female imago are less degenerate, but are nevertheless out of all proportion to the broad antennæ of the female pupa (compare figs. 17 and 15). The male antennæ form most highly complex and expanded sense-organs (fig. 16), while the corresponding pupal antennæ are not much larger than those of the female pupa (compare figs. 14 and 15). The details of the antennæ of both sexes are shown in figs. 18 and 19.

Again, the antennæ of the female *Cerura vinula* exhibit distinct pectination like that of the male, but on a decidedly smaller scale; while the pupal antennæ are more nearly of the same size (compare figs. 20, 21, 22, and 23).

Even the extremely degenerate females of the genus *Fumea* emerge from pupæ with tolerably stout and well-developed antennæ (Plate XXVII. fig. 14). The lowest depth of female degeneration is reached in those Psychids which are a mere bag of eggs, without limbs or sense-organs, and utterly unable to emerge from the pupal shell. Distinct traces of antennæ can nevertheless be made out upon the pupæ of some of them (Plate XXVII. fig. 15, A).

The same facts are well seen among the degraded females of certain *Geometræ*. The wingless female of *Nyssia zonaria* possesses thread-like antennæ very different from those of the male, but the pupal antennæ do not greatly differ in size (compare Plate XXVI. figs. 24, 25, 26, and 27). The similarly degenerate female of *Hybernia defoliaria* emerges from a pupa with comparatively broad antennæ (compare Plate XXVII. figs. 8 and 9).

2. *The History of the Degeneration of the Antennæ in Female Imagines.*—These and other examples could be easily arranged in a series leading from a state of sexual equality through stages of increasing female degradation to the culmination reached in the condition of many Psychids. It appears certain that all such cases of sexual inequality have been gradually reached by the degeneration of one sex attended by a corresponding development of the other. The tendency towards such a change is present in many groups of moths, especially among the Bombyces, and exists whenever the females are less active than the males. When this is the case, the chief competition among the males will be in sense-organs to ascertain the existence of virgin females at as great a distance as possible, and in the power of flight to reach the female before other males. But such competition, ensuring the success of the best-endowed males, and a gradual improvement from generation to generation in their sense-organs and their powers of flight, will therefore cause coitus to take place at a shorter and shorter interval after the emergence of the female from the pupa. But such a result must tend

towards the degeneration of the female sense-organs, because, as the organism becomes more and more sluggish, the necessity for these organs diminishes both for sexual and for other purposes. The reverse takes place in the male, as the sense-organs become specialized for sexual purposes. It is likely that such specialization implies a partial restriction and not an actual limitation of function, the antennæ still remaining sense-organs of very general use, although their high development is related to one out of many possible functions.

It is obvious that the diminution in the activity of one sex must in certain cases involve other organs in addition to the antennæ. These will be considered in the next Part, and will be found to throw further light upon the subject of the present Section.

Part V.—The Pupal Wings.

1. *The Relation of Pupal to Imaginal Wings.*—Considering the conclusions already arrived at by the comparison of pupal and imaginal antennæ,—that when an imaginal organ falls into disuse and shrinks, the corresponding pupal organ shrinks at a very much slower rate, and so presents a picture of the long-past condition of the former—it became very probable that a similar relation would be found to obtain in other sets of organs, and especially the wings. I have already shown that the function of the wings bears a close relationship to that of the antennæ.

My attention was first called to this comparison between pupal and imaginal wings in species of which the females possess these organs in a very rudimentary form, by the study (in 1885) of the remarkably degenerate female pupæ and imagines of *Fumea nitidella*. Although the males of this species are active bombyciform moths, the females are exceedingly degenerate, never leaving the case in which the pupa was contained, but sitting upon the end of it for their whole life. In this position they deposit their eggs in the empty pupal shell within the case from which they themselves emerged. Corresponding to this sedentary life, the wings are reduced to minute tubercles, so small as readily to escape detection, and having neither the shape nor appearance of wings. On examining the female pupa I saw at once that it possesses small but distinct wings of characteristic structure and shape, and with the normal relation to the other appendages and to the meso- and metathoracic segments (Plate XXVII. fig. 14). The male pupa is shown in figs. 12 and 13.

This comparison is exceedingly interesting, for it at once disposes of the view that the rudimentary wings of such females as these are not due to degeneration from a winged condition, but are remnants of truly ancestral, partially developed structures. This view is also rendered equally improbable by other considerations. Thus, it has already been shown, by means of the pupal antennæ, that such females formerly resembled the males to a greater extent than at present in one set of rudimentary organs, suggesting that other sets have had a similar history. Furthermore, we must probably look for the origin of wings in some of the suppressed stages which preceded that represented by the pupa, inasmuch as pupæ always possess wings; and it seems certain that these organs originally arose in the phylogenetic development after the manner which is indicated by the ancestral Orthoptera—namely, that they arose gradually, as their slowly unfolding structure rendered possible the transition from the slight prolongation of a jump—their first locomotive function—into the sustained movements of true flight. If these arguments be correct, it is clear that fairly-developed wings such as pupæ possess are very far from representing the original condition of these organs, while the rudimentary wings of certain imagines are clearly due to degeneration.

In order to test further the conclusions arrived at by studying *F. nitidella*, I made use of another very common species of which the females have rudimentary wings, viz. *Orgyia antiqua*. After emergence from the pupa the female moths sit on the outside of their cocoons, which they never leave, but deposit their eggs upon the surface of the silk. Although very degenerate, they possess distinct wings of the usual shape, though very small and quite useless. The size and shape of the left fore wing are shown in Plate XXVII. fig. 11. I then examined the pupal wings and found that, although very much smaller than those of the male, they are considerably larger than the wings of the female moth, as is seen by comparing figs. 10 & 11, Plate XXVII., both figures being magnified to the same extent. Hence we find precisely the same relation between the wings of the male and female pupa, and between those of the latter and of the female imago, as in *Fumea nitidella*, although degeneration has gone further in the last-named species.

Some of the more degenerate *Psychidæ* were then selected for examination. In these the female imago is a mere bag of eggs, and remains permanently enclosed in the pupal shell. In the majority of female pupæ examined, the lost imaginal parts—wings, legs, antennæ, &c.—are evidently represented by confused creases on the corresponding parts of the cuticle. In one unnamed species, kindly lent me by my friend Mr. W. White, the pupa retained far more distinct traces of structures formerly possessed by the imago. The anterior part of the pupa is represented in fig. 15, Plate XXVII., and it is seen that the wings are distinct as small pouches on the meso- and metathorax, that the legs, antennæ, and even the eyes and mouth-parts can be plainly made out, although of a very rudimentary nature. The moth itself appears to be as degenerate as any Psychid in which the traces of lost parts upon the pupa are far more obscure. The figure also shows that the pupal prothorax splits along the median dorsal line and that the hairs of the enclosed imago are seen through the opening, so that the first part of the process of emergence from the pupa appears to be recapitulated in this most degenerate form.

Further examination of various species in which the female imagines possess rudimentary wings also supported the conclusion that such degeneration is of recent date.

Thus many species of *Geometræ* were investigated. The minute functionless wings of a female of *Cheimatobia boreata* were found to retain distinct traces of the colours and patterns which are characteristic of the functional wings of the male, thus supporting the conclusion that the reduction in size is very recent. The wings of a female of the closely-allied *Cheimatobia brumata* were found to be much smaller, with far less distinct indications of pattern (compare figs. 1 & 2, Plate XXVII.). The wings of the female *Hybernia progemmaria* are less reduced than those of *Cheimatobia*, although quite useless for flight. The wide individual differences between the females of this species in pattern, shape, size, and character of the fringe are also evidence of recent degeneration (compare figs. 3, 4, 5, & 6, Plate XXVII.). Even stronger evidence is, however, supplied by the closely-allied *Hybernia defoliaria*, of which the female imagines are usually described as entirely wingless. Minute rudiments of wings can, however, be detected (Plate XXVII. fig. 9). Corresponding to the reduction in the wings, the legs are of great size, being of the utmost importance for locomotion. Comparison between *H. defoliaria*, *H. progemmaria*, and the other species of the genus *Hybernia*, proves that the reduction of the wings has been carried to very different points in species which are nevertheless closely allied. The wings of a female pupa of *H. defoliaria* are shown in Plate XXVII. fig. 7, magnified to the same extent as the imago (fig. 9). In spite of the degenerate condition of the imago, the pupal wings are seen to be large and well-formed, and are in fact almost equal to those of the male pupa. The same facts hold for another Geometer, *Nyssia zonaria*, in which the wings of the female are extremely minute (Plate XXVI. fig. 28), although the difference between the wings of the pupæ of the two sexes is quite inconsiderable (compare Plate XXVI. figs. 24 & 25).

When we compare the pupæ of the degenerate Geometers with those of the Bombyces, we find evidence for a more rapid and recent change in the former. Thus the degeneration of the latter is of sufficiently long standing to have caused the wings of their female pupæ, such as those of *Orgyia*, *Fumea*, and especially *Psyche*, to become decidedly reduced in size. This is evident when we compare the pupal wings of, *e. g.*, the female *Fumea* (Plate XXVII. fig. 14) with those of the male of the same species (fig. 12). The immense difference between the results of such a comparison and that instituted above in the case of *N. zonaria* (Plate XXVI. figs. 24 and 25) or *H. defoliaria* proves that the degradation of the latter is of far more recent date.

The comparison between pupal and imaginal wings in species with degenerate females indicates that Professor Moseley's conclusions require some modification; for in some of the species the pupal organs have shrunk as the corresponding imaginal organs have diminished, although the former have changed at a much slower rate. Hence we are driven to conclude that the particular shape and size of a pupal organ, which at any one time fits an imaginal organ developed within it, will not be retained indefinitely upon the shrinkage of the latter, as Professor Moseley was led to believe from his observations upon the antennæ, but that the pupal organ will also eventually become smaller. At any rate, this has been the case with the pupal wings. I do not think that at present there is any evidence for believing that the female pupal antennæ have yet shrunk like the wings; for the former, although smaller than the same organs in the male pupæ, may nevertheless have been at no time larger than at present. Such a conclusion is supported by the arguments in the last division of the subject, in which it was shown to be very probable that the male imaginal antennæ have increased as the female organs have diminished, so that the pupal organs of the former must have undergone recent increase, while the female pupal antennæ may indicate the size of these organs in both sexes, before degeneration of the one, and concomitant development of the other, commenced. Or, considering how very common it is among moths for the male antennæ to be more developed than those of the female, only part of the sexual differences between pupal antennæ may date from the beginning of the rapid degeneration and development which certain species have undergone in the two sexes respectively. But it is most likely that the general and widespread difference between these imaginal organs in the two sexes is due to precisely similar causes acting slowly and only up to a certain point—due, in fact, to the competition among the males being keener than that among the females. When the two sexes seem to approach most closely in respect of this competition, flying together and both apparently exercising the powers of active selection—when courtship appears to be mutual—then the differences between the antennæ of the two sexes become very small, and in the cases of most complete equality disappear altogether. And it must be remembered that the antennæ are in all probability sense-organs of very general use, although their sexual function is by far the most important, and that free and active flight gives abundant opportunity for their exercise in all possible directions, so that these organs may be sometimes equally developed in the two sexes, when they may be more especially used in courtship by the males.

Returning to the pupal antennæ of degenerate females, the observations upon the wings of the same species render it likely that the former will slowly diminish in size, although they have probably not done so at present, except, indeed, in the most degenerate species, viz. many *Psychidæ*. The pupal wings may have shrunk earlier, because they form organs of considerable size, and their shrinkage therefore especially favours a corresponding increase of other parts. The degeneration of the imaginal sense-organs and organs of locomotion is generally accompanied by an increase in the size of the abdomen, which becomes relatively larger than in the more normal females. Thus the number of eggs is often largely increased, while the additional weight is not too great a strain upon the comparatively passive organism. In certain species the legs are also specially developed in order to bear more than their ordinary share in locomotion—*e. g.* in certain Geometers, such as *H. defoliaria* (Plate XXVII. fig. 9).

2. *The History and Causes of Degeneration in Female Imagines of Lepidoptera.*— It is now possible to give a more complete account of the history of degenerate females than could be advanced from the consideration of the antennæ alone. Starting from the condition of nearly equal powers of flight and equally developed sense-organs in the two sexes, we find the first indications of divergence in the antennæ, which are commonly more developed in the males because of their activity in courtship; but in the majority of moths the females remain active organisms with considerable powers of flight, which are used especially in connexion with the deposition of eggs and for obtaining food. The first of these important functions may be fairly looked upon as balancing the chief necessity of male flight, *i. e.* to reach the females. Nevertheless, there is this important difference, that the flight of the males tends to become very rapid, because of the stress of competition, while there is no such strong tendency in flight which is used for oviposition. On the other hand, in the flight which is employed for food, the females are as subject to competition as the males, and, accordingly, we find that it is the rule among the great groups of feeding moths (the Geometers and

Noctuas) and among the butterflies that the powers of flight in the two sexes are not very unequal.

The same conclusions are supported even more strongly by looking a little further into details. Among the *Sphingina* (adopting the arrangement of Stainton's 'Manual') there is no marked difference between the flight of the sexes in the flower-haunting, day-flying *Zygænidæ*, *Sesiidæ*, and *Ægeriidæ*. In the *Sphingidæ*, which feed, both sexes fly actively; while in the species of the genus *Smerinthus*, which do not feed, both sexes are sluggish, but the females more so than the males. In the *Bombycina* very few of the moths feed, and the males are nearly always extremely active fliers and the females very sluggish: the exceptions are especially interesting. The *Lithosiidæ* feed eagerly and are commonly taken at sugar, and the females fly actively with the males; the same facts are true of a few flower-haunting genera among the *Cheloniidæ*, in which both sexes fly by day. I do not know of any other Bombyx which feeds except *Cossus ligniperda*, which, I believe, has been occasionally seen at sugar; and in this species both sexes are sluggish. In the great majority of the rest of this group flight among the females is almost or entirely subservient to oviposition, while that of the males is far more active and in many species has been rendered extremely rapid by competition in the struggle to reach the females. The female moth is nearly always at a disadvantage in flight as compared with the male because of her relatively large and heavy abdomen filled with eggs. This cause, always present to some extent, tends to produce important results as soon as a species ceases to feed in the perfect state, and can therefore dispense with rapid flight in the females. Increase in the size of the abdomen will then be an advantage, enabling the female to lay more eggs or larger ones—in either case benefiting the species in the larval state—while greater sluggishness of flight only affects the rate of oviposition. Furthermore, the danger resulting from slow oviposition may be met in special ways.

By the working of this cause, rendered effective by the cessation of feeding, we meet the first strong indications of degeneration in those females which fly sluggishly to deposit their eggs, but for no other purpose. In such cases it is not uncommon for the females to fly at a different time from the males. Thus the males of *Lasiocampa rubi* fly with great rapidity in bright daylight, while the females sit perfectly motionless, but in the evening they fly slowly and deposit their eggs. I know this to be the case from my own experience, and I have no doubt that it is the same with *Endromis versicolor*, *Saturnia carpini*, and others *. The only doubt is as to the evening flight of the females; for in other respects these two species are well known to behave in the same manner as *L. rubi*. The flight of such females, although sluggish, is still necessary, except under certain conditions. The *Bombycinæ* are generally large moths, and there would be a two-fold danger in depositing all the eggs in one place—that of insufficiency of food and easy detection by enemies (unless indeed the larvæ were well concealed or defended by a disagreeable taste or smell), and the latter, the chief difficulty, applies to small as well as large moths. But while further degeneration is thus rigidly prevented in most cases, there are certain moths which escape from the limiting conditions.

* Weismann states that the females of *Aglia tau* deposit all their eggs in one spot, being unable to fly on account of the weight of the abdomen. The males, on the other hand, fly swiftly, seeking for the females. ('Essays on Heredity,' Clarendon Press, 1889, pp. 17, 18.)

The two species of the genus *Orgyia* are small moths as compared with the majority of Bombyces: the larva of one species (*O. antiqua*) eats almost anything, while that of the other (*O. gonostigma*) feeds on large trees; and it is known that in the former case the eggs do not all hatch at once, but produce larvæ in batches over a period of ten weeks. Furthermore, the larvæ are brightly coloured, and possess "tussocks" and eversible glands as defensive structures; and it is known that they are disagreeable to certain insect-eating animals. Hence the species of this genus have escaped from the conditions which render flight necessary for oviposition, and the eggs are laid all over the cocoon. The female moth has an immense abdomen, and therefore can lay a very large number of eggs, so as to ensure that many larvæ shall reach some food-plant. The degenerate wings and antennæ of the commoner species have been already described and compared with the less degenerate organs of the pupa, and the antennæ with those of the male. Another family of the *Bombycinæ* are even more degenerate—the *Psychidæ*: many of these escape from the above-mentioned conditions by their extremely small size, and all of them are specially defended because their larvæ live in cases, and are therefore protected against many foes. Furthermore, the larva-case, in or upon which the female moth always remains, is fixed to the food-plant, so that there is no chance of the larvæ wandering. The food-plants (when known) are amply large enough for the small larvæ to feed upon without fear of starvation. The wings of the female of one of the less degenerate species (*Fumea nitidella*) have been described and compared with those of the pupa (Plate XXVII. fig. 14). The examination of the pupa of one of the more degenerate species (fig. 15) renders it equally clear that the female imago has undergone degradation from a more perfect condition.

Hence the causes of degeneration among the females of the *Bombycinæ* appear to be sufficiently clear. Equally degraded forms are also met with among the *Tineina* and the *Geometrina*. Of the former no more need be said, for everything that has been said of the *Psychidæ* applies to them.

Among the Geometers degenerate females with functionless wings are met with in 5 genera—*Phigalia* (1 species), *Nyssia* (2 species), *Hybernia* (5 species), *Anisopteryx* (1 species), and *Cheimatobia* (2 species). The circumstances under which such females appear in this large group of feeding moths support the explanation which is offered above. The first two genera include Bombyciform moths, of which the males have much-feathered antennæ while those of the female are thread-like. I think it is very probable that they do not feed, and the moths make their appearance at a time of the year which does not encourage feeding by providing many different kinds of bloom, although plenty of food exists for those moths which need it; besides, the low temperature itself tends towards inactivity when flight is unnecessary. *P. pilosaria* appears in February and March: its larva feeds on oak. *N. zonaria* appears in September in the North of England: its larva feeds on yarrow. *N. hispidaria* appears in February and March, and the larva feeds on oak. The same explanation (season) holds with even more force for the next three genera. In the genus *Hybernia*, as the name implies, the perfect insects emerge in the winter. *H. rupicapraria* appears in January and the first half of February: the larva feeds on whitethorn, blackthorn, and oak. *H. leucophearia* appears in February and March: the larva feeds on oak. *H. aurantiaria* appears in October and November: the larva feeds on whitethorn, birch, and oak. *H. progemmaria* appears in February and March: the larva feeds on hornbeam; and *H. defoliaria* appears in October: the larva feeds on many trees. In the genus *Anisopteryx*, *A. æscularia* appears in April, and the larva feeds on many trees. Lastly, in the genus *Cheimatobia*, *C. brumata* appears in October, November, and December: the larva feeds on nearly every kind of tree; while *C. boreata* appears in October, and the larva feeds on birch. No one of these species appears on the wing before September or after April, while most of them assume the perfect state in the coldest part of the year. Furthermore, the difficulties in connexion with oviposition do not obtain here; for the female moths leave their cocoons and crawl upon the food-plants of the larva, depositing their eggs in appropriate situations as readily, although not as rapidly, as if they were able to fly. The legs of many of these females are specially developed, thus facilitating locomotion (see Plate XXVII. fig. 9). Furthermore, the moths are not large, and generally lay their eggs upon large trees or upon food-plants such as yarrow, which are very numerous, and which grow in close proximity to one another, so that there is little fear of starvation, even when the eggs are laid near together.

Considering all these facts, it appears most probable that the wings became functionless in certain female moths which appeared in the colder months of the year and did not require the use of these organs for feeding, for courtship, or for oviposition. Furthermore, the wings when useless would be encouraged to shrink by a variety of causes, of which a probably important one is the fact that the females would be much more conspicuous during oviposition if they crawled about with a surface immensely extended by means of these organs. But there has also been the same cause acting thoughout which was pointed out as of the first importance in the *Bombycinæ*—the advantage which the species gains from the possession of a large abdomen by the female. The difference in size between the male and female abdomen in these moths is far greater than in any other species in the *Geometrinæ*. The last is doubtless the great cause of degeneration in all cases, and among this large group of feeding moths the temperature has indirectly produced such results in a few species by the discouragement of feeding, so that the chief cause could come into operation, receiving accessory aid from the positive protective gain which would result from the loss of functionless wings.

It is hardly necessary to point out that the degenerate condition of the females renders certain a keen competition among the males, which ensures the continued possession of the power of flight in this sex, notwithstanding the low temperature and indifference to food. It is well known, however, that another condition may render the wings functionless, even in the male sex, *i. e.* existence upon islands in very stormy areas where high winds recur constantly. But this cause is not efficient in Great Britain, and no such effect is witnessed in our Lepidopterous fauna.

It is quite clear that the initial stages of diminution, however caused, in functionless wings would not affect the corresponding pupal organs, because the latter are very much smaller than those of the imago, the difference in size being due to expansion immediately following emergence from the pupa. We should not therefore expect any shrinkage in the pupal wings until the imaginal organs had become smaller than the former. The various stages of shrinkage are well exemplified in the genus *Hybernia* alone. In *H. progemmaria* the wings of the female are certainly far larger than those of the pupa; in fact the expansion does take place, but it is much limited; and the resulting organs are entirely useless. In *H. rupicapraria* and *H. aurantiaria* the wings seem to be as nearly as possible of the same size as those of the pupa: the wings of the female *on emergence* are of the same size as those of other females, but there is no expansion. Finally, in *H. leucophearia* and *H. defoliaria* the wings of the female are almost invisible and much smaller than those of the pupa. In this last case alone is there any probability of the pupal wings having shrunk, and I should imagine that such shrinkage, if any, would be small, because the transition described above in nearly allied species belonging to one genus seems to show that the whole character is very recent. Since writing this sentence, I have been enabled to obtain evidence of the validity of the conclusion; for I have now shown that the pupal wings of the female *H. defoliaria* remain of considerable size (Plate XXVII. fig. 7).

I wish to point out clearly how much and how little is contained in this explanation and history of degeneration. I have shown the causes which always tend in this direction and the chief conditions which prevent their action. I have pointed out that certain species become partially, others completely, relieved from these conditions, and thus seem to be free to follow the tendencies, and we see that all the instances of degeneration occur among such species. But while it has thus been, I think, sufficiently explained how it is that degeneration of the female wings becomes possible, it is quite a different thing to say why certain species and not others should have availed themselves of the possibility. There are certain other small species of *Bombycinæ* and *Tineinæ* to which degeneration seems to be as possible as to those in which this change has actually occurred. The probable answer is a very general one—that the struggle for existence would prevent a large number of species from taking one uniform line of development, even though it may appear beforehand to be very directly pointed out as the path of least resistance for all of them. Furthermore we may fairly concede that in many instances it is now impossible for us to ascertain the exact conditions which led certain species to take the line we are considering to the exclusion of others, to which it was also open, as far as the general conditions would admit. In the *Geometrinæ*, however, I think I may claim that the demonstration of the cause and course of degeneration has been complete. The number of species to which the line was open being limited, they appear almost without exception to have availed themselves of the opportunity.

3. *The Form of the Imaginal Fore Wing detected on that of the Pupa.*—Although the wing of the imago expands into a size far beyond that reached by the pupal organ within which it is developed, the former does not entirely fill the latter before emergence. The margin of the imaginal wing lies well within the corresponding margin of the pupal wing which encloses it. Not only are the two margins separated by an interval, but their contours are frequently very different. Furthermore, in many species the position of the future margin of the imaginal wing can be distinctly made out on the pupal

surface from the very beginning of the pupal period and long before the imaginal organs have begun to appear. The line which corresponds to the future imaginal hind margin is especially distinct, and is separated from the hind margin of the pupal wing by a very wide interval.

These facts were shown in the plate accompanying my paper in the Phil. Trans. Roy. Soc. vol. 178 (1887), B, pp. 311–441, and were briefly alluded to in the description of figure 11 (p. 440), which represented a dark variety of the pupa of *Vanessa Io*, on which the imaginal hind margin is very distinct.

These facts are probably true of the hind wing as well as the fore wing, but they have only been studied in the latter.

Over the part of the pupal fore wing beneath which the imaginal wing will develop, lines which correspond to the future venation are more or less plainly visible. These lines cease at the limits of the area over which the wing will be formed (viz. the line H′.M′. in figs. 18, 22, &c. on Plate XXVII.). Sometimes, however, their direction is continued by irregular lines of pigment across the interval between the pupal and future imaginal hind margins (viz. between H.′M.′ and H.M.). These irregular continuations are, however, very different in character from the more defined appearance of the lines which represent the venation. When the latter are studied in especially favourable species (*e. g.* in *Vanessa Atalanta*, fig. 18, Plate XXVII.), they are seen to correspond exactly with the future venation of the imaginal wing. This is all the more remarkable inasmuch as the main tracheæ within the pupal wing, which will ultimately be enclosed as important elements in the imaginal veins, possess at this time an arrangement different from that which they will then assume. Thus fig. 26, Plate XXVII., shows the arrangement of the main tracheæ in the left hind wing of the pupa of *Papilio Machaon*, as seen from within, an arrangement very different in detail from that which will be subsequently assumed and is already mapped out (in the case of the fore wing) upon the pupal cuticle.

It has been already found that indications of earlier imaginal conditions may be traced in the structure and form of the pupa. It was therefore of interest to investigate from this point of view the relation of these pupal markings to the form and appearance of the imaginal wing. The point which I selected as a test was the indented and irregular form of the hind margin of the fore wing in *Vanessa* and allied genera. There is every reason for the belief that such an outline has been derived from the more usual smooth and continuous form of margin. A careful comparison of the imaginal hind margin with that marked out on the pupa supported this conclusion.

The hind margin of the fore wing of the imago of *Cynthia cardui* presents a slight bay in its central part (fig. 17, Plate XXVII.); but the bay is even less marked in the corresponding line upon the pupa (H′.M′., fig. 16). In other words, the latter is more normal and is now in a stage through which the imaginal hind margin has passed. Some indications of the black-and-white fringe on the imaginal hind margin (fig. 17) can be made out in the disposition of the pupal cuticular pigment along the corresponding line (H′.M′., fig. 16). Similarly in *Vanessa Atalanta* the bayed hind margin of the imago is less pronounced on the corresponding part of the pupa (compare fig. 19 with fig. 18, H′.M′.). A similar relationship is witnessed in *Vanessa Io* (figs. 20 and 21), although the difference is rather in the angularity and amount of projection of the cusps than in the depth of the bay. In dark varieties of this pupa the pigment is distributed along the line H′.M′. (fig. 20) in such a manner as to suggest a former black-and-white fringe, which is now absent from the imaginal hind margin. The dark parts are diagrammatically indicated in the figure by thickenings along the line H′.M′., and their position will be found to correspond with the dark parts of the imaginal fringe in *C. cardui* (fig. 17) and *V. Atalanta* (fig. 19). Inasmuch as these latter species are more ancestral than *V. Io* as regards the comparatively slight degree of indentation of the hind margin, and especially as regards their markings *, it is most probable that *V. Io* at one time also possessed a black-and-white fringe, which is still indicated in the corresponding part of the dark pupæ of this species. A comparison between the pupa and imago of *V. polychloris* (figs. 22 and 23) similarly shows that the pupal line H′.M′. is rather less indented than that of the imago.

Finding these results in our common *Vanessidæ*, I was extremely anxious to test them by an examination of the allied *Grapta C-album*, which possesses a far more jagged hind margin than any other British butterfly. After searching in various directions, I obtained an empty pupal shell of this species, through the kindness of my friend Mrs. Luard. An examination of this pupa supported in the most complete manner the conclusions already arrived at. It is clear that the hind margin of the imago (fig. 25) is far more jagged than that of the corresponding line upon the pupa (H′.M′., fig. 24), which indeed is not much in advance of the condition found in the imago of *V. Io* or *V. polychlorus* (figs. 21 and 23).

Hence we see that not only are the traces of lost imaginal wings preserved, but the indications of ancestral forms and markings are also fixed on the surface of the pupa. Furthermore, the results of this investigation suggest that further work along the same lines will reveal many other interesting conclusions as to recent changes which have taken place in the imago.

In conclusion, I desire to thank those friends who have kindly supplied me with material for this paper. Mr. W. White especially has lent me many specimens which have been of the greatest service. Professor Meldola has carefully been through most of the manuscript with me, and has offered many valuable suggestions.

* See Dr. F. A. Dixey's admirable paper "On the Phylogenetic Significance of the Wing-markings in certain Genera of the *Nymphalidæ*," Trans. Ent. Soc. Lond. 1890, pp. 89–129.

DESCRIPTION OF THE PLATES.

PLATE XXVI.

The Antennæ of Lepidopterous Pupæ compared with those of the corresponding Imagines.

All the figures are rather smaller than the sizes indicated by the stated amounts of enlargement. The figures were reduced by the lithographer, but the deviation from the originals does not appear to exceed 7 per cent. in any case, and is often much less.

Fig. 1. ×2. The left antenna of a male pupa of *Saturnia carpini*. The transverse markings are more numerous than in the figure.

Fig. 2. ×2. The left antenna of a female pupa of *Saturnia carpini*.

Fig. 3. ×9. The left antenna of a male imago of *Saturnia carpini*, as seen from its upper surface, showing the complexity of this sense-organ. Each joint of the antenna is seen to possess two rami upon each side; these are thickly clothed with sensory hairs (only shown on one side) arranged so as to expose a wide surface to the air. The high degree of development reached by the male antenna corresponds to the size of the pupal antenna within which it is formed (fig. 1).

Fig. 4. ×9. The left antenna of a female imago of *Saturnia carpini*, as seen from its upper surface. The organ is very degenerate in size and structure (the latter studied better in figs. 5 and 6), and is out of all proportion to the pupal antenna within which it is formed (fig. 2). The comparison suggests that the degeneration of the sense-organ of the female imago is comparatively recent, so that the pupal organ has not had time to shrink to a corresponding degree. Only a single much diminished ramus can be seen on each side of each joint of the antenna, but traces of a second can be made out on some of the joints by the use of a higher power (fig. 5).

Fig. 5. ×50. Right antenna of the female imago of *Saturnia carpini*. The sixth and seventh joints above that upon which traces of rami could first be made out in ascending from the basal joint. The joints are represented as seen from below. The longer rami on the left side are directed posteriorly and inferiorly in the natural position of the organ. Thinly scattered sensory hairs are placed upon the rami and the adjacent part of the joints; they are chiefly developed in connexion with the longer rami. In front of (viz., above in the figure) the longer ramus on the lower joint there is a distinct trace of the second ramus in the form of a tubercle bearing a long bristle; a less distinct tubercle without a bristle is seen on the corresponding part of the upper joint. It is therefore clear that the longer rami correspond to the posterior pair on each joint of the male organ.

Fig. 6. ×50. Right antenna of another female imago of *Saturnia carpini*. The joints correspond to those shown in fig. 5, and they are seen from the same point of view. The individual being larger than that from which fig. 5 was taken, the joints are far thicker and larger, although the degeneration has proceeded much farther. Thus the rami are much shorter on both sides, there is no trace of an anterior ramus, and the number of sensory hairs is decidedly smaller, especially on the right side. This great fluctuation in the degree of degeneration supports the conclusion that the latter is of recent date, a conclusion confirmed by a study of the pupal antennæ (figs. 1 and 2) in relation to those of the imago.

Fig. 7. ×7. The anterior part of a male pupa of *Aglia tau*, as seen from the ventral aspect. The enormously broad pupal antennæ occupy a very large area. The character of the surface is only indicated on the left side.

Fig. 8. ×7. The anterior part of the female pupa of *Aglia tau*, as seen from the ventral aspect. The pupal antennæ are very large, although they do not approach the size reached in the male. The median ridge is pronounced, and probably corresponds to the part occupied by the

imaginal antennæ during development and just before emergence. The character of the surface is only indicated on the left side.

Fig. 9. ×7. The left antenna of the male imago of *Aglia tau,* as seen from above and behind. The fine sensory hairs are not indicated. The organ is seen to be even larger than that of the male *S. carpini* (fig. 3). The enormous size of the imaginal organ corresponds with that of the pupal organ within which it is developed (fig. 7).

Fig. 10. ×7. The left antenna of the female imago of *Aglia tau,* as seen from above and behind. Just as the male organ is larger, the female organ is smaller than in *S. carpini* (fig. 4), indicating that the degeneration of one sex has gone hand-in-hand with an increase in the powers of the other. The recent date of the degeneration is well seen when we compare the size of the imaginal organ with that of the pupal organ within which it is formed (fig. 8).

Fig. 11. ×50. The terminal part of one of the posterior rami from a joint of the antenna of the male *Aglia tau.* Each joint bears two pairs of rami (fig. 9), of which the posterior are larger and more complex. The figure shows the long curving sensory hairs and the three terminal bristles. Both hairs and bristles are foreshortened.

Fig. 12. ×50. The terminal part of one of the anterior rami from a segment of the antenna of the male *Aglia tau.* The figure shows the long curving sensory hairs, which are turned towards those of the posterior ramus of the segment in front. The arrangement of the rami is shown in fig. 9, where they are seen to form pairs on each side of the middle line, made up of the anterior rami of one segment placed opposite to the posterior rami of that in front of it. The length of the sensory hairs is more fully shown in fig. 12, because they are seen from the side. Figs. 11 and 12 show that the male antenna of *Aglia tau* is extremely complex, and the arrangement is such as to render it an unusually efficient organ for sifting a large quantity of air, so that the faintest trace of odour may be detected.

Fig. 13. ×50. Two of the most fully developed segments from the right antenna of the female *Aglia tau,* seen from below and in front, in such a position that the rudimentary sensory hairs of the posterior inferior border are in profile. The male antenna is more complex than that of *S. carpini*; but this figure shows that the degeneration of the female has been carried far beyond the point reached by the female *S. carpini* (compare figs. 5 and 6). The rami represent the posterior pairs of the male organ. Those of the posterior inferior border possess two terminal bristles, while those of the other border only possess one. The difference between the size and arrangement of the sensory hairs in male and female is very striking.

The arguments as to the recent date of the degeneration of the female, derived from *S. carpini,* are thus confirmed and extended by an examination of *Aglia tau.*

Fig. 14. ×9. The outline of the left pupal antenna of the male *Orgyia antiqua.*

Fig. 15. ×9. The antennæ, limbs, &c. of the female pupa of *Orgyia antiqua.* The pupal cuticle had been mounted for the microscope, so that the structures were somewhat flattened. The antennæ are seen to be broad and well developed, although much smaller than those of the male.

Fig. 16. ×9. The antenna of the male imago of *Orgyia antiqua,* showing the great size and complex structure. The development of the organ corresponds with that of the pupal antenna, as in the males of *Aglia* and *Saturnia.*

Fig. 17. ×9. The antenna of the female imago of *Orgyia antiqua,* showing an extremely degenerate condition. As in *Aglia* and *Saturnia,* the corresponding pupal organ has a size which is utterly disproportionate to that of the thread-like and rudimentary structure developed within it.

Fig. 18. ×50. A segment from the middle of the antenna of the male imago of *Orgyia antiqua.* Although inferior in complexity to the corresponding organ of *Aglia* and *Saturnia,* the structure is extremely elaborate. The rami, of which there are a single pair on each segment, are seen to be abundantly covered with sensory hairs, and to possess three terminal bristles.

Fig. 19. ×50. The seventh and eighth segment (from the base) of the antenna of the female imago of *Orgyia antiqua*. The structure is seen to be very degenerate; the small rami possess two terminal bristles, but no traces of sensory hairs are seen.

Fig. 20. Natural size. The left antenna of the male pupa of *Cerura vinula*.

Fig. 21. Natural size. The left antenna of the female pupa of *Cerura vinula*.

Fig. 22. Natural size. The left antenna of the male imago of *Cerura vinula*.

Fig. 23. Natural size. The left antenna of the female imago of *Cerura vinula*. It is very interesting to find that the same relation as that illustrated above, between degenerate female antennæ and the corresponding pupal organs, also obtains in species where the degeneration is comparatively slight.

Fig. 24. ×5·25. The male pupa of *Nyssia zonaria*, as seen from the left side and also somewhat from the ventral aspect. The pupal antennæ are seen to be large.

Fig. 25. ×5·25. The female pupa of *Nyssia zonaria*, seen from the same aspect. The pupal antennæ and wings, although smaller than those of the male, are seen to be well developed.

Fig. 26. ×9. The left antenna of the male imago of *Nyssia zonaria*, as seen from above. The upper rami are distinctly shown, the lower only for part of the length of the organ.

Fig. 27. ×9. The left antenna of the female imago of *Nyssia zonaria*, as seen from above; the number of rings indicated is only approximately correct. The curvature of the antenna was the reverse of that in the male, although this difference is compensated in figs. 26 and 27 by the base of the male antenna being placed over the tip of that of the female and *vice versâ*. The degeneration of the female antenna is seen to be very complete, although the corresponding pupal organ is by no means small.

Fig. 28. ×5·25. The left fore wing of the female imago of *Nyssia zonaria*. The minute size of the structure is well shown, especially when it is compared with the corresponding part of fig. 25, which is magnified to an equal extent. Here also we meet with evidence that the degeneration of the female wing is very recent; for the pupal wing is but little smaller than that of the male, within which fully formed and functional wings are developed.

Fig. 29. ×50. The antenna of the larva of *Pieris brassicæ*. The figure is added for comparison with the details of the imaginal and pupal antennæ shown upon this Plate.

Plate XXVII.

The Wings of Lepidopterous Pupæ compared with those of the corresponding Imagines.

All the figures have been unavoidably reduced by the lithographer, and are much smaller than the sizes indicated. The deviation from the originals appears to be about 15 per cent.

Fig. 1. ×7. The left wings of the female imago of *Cheimatobia boreata*. Although the wings are very small and of course utterly useless, the figure shows that they retain distinct traces of a pattern which suggests that developed upon the functional wings of the male. This is an indication of recent degeneration.

Fig. 2. ×7. The left wings of the female imago of *Cheimatobia brumata*. The wings being far more degenerate than those shown in the last figure, the pattern is much less distinct.

Figs. 3, 4, 5, & 6: all ×7. The left wings of four female imagines of *Hybernia progemmaria*. The individual differences in size, shape, and in the length and character of the fringe are seen to be very marked. The markings, not represented in the figures, were also very different. This great individual difference also points to recent degeneration from a more highly developed condition.

Fig. 7. ×8. The outline of the left wings of a female pupa of *Hybernia defoliaria*. Although the imaginal wings are very unusually degenerate (see fig. 9), those of the pupa are seen to be well formed and of considerable size. The margin of the hind wing is distinctly seen in its normal position, parallel with the dorsal margin of the fore wing, and occupying the right side of the figure. A comparison of figs. 7 and 9 points to the very recent date of the degeneration of the wings in the females of the genus *Hybernia*.

Fig. 8. ×8. The outline of the left antenna of the female pupa of *Hybernia defoliaria*, shown in the last figure. The antenna is seen to be broad and well developed, and out of all proportion to the filiform degenerate structure which is formed within it (compare fig. 9).

Fig. 9. ×8. The head and thoracic segments of the female imago of *Hybernia defoliaria*, as seen from the left side. The moth represented in this figure emerged from the pupa, parts of which are represented in figs. 7 and 8. The antennæ are thread-like and degenerate, and the wings are so small that they are usually considered to be altogether absent. They are shown in the figure as minute pouch-like extensions of the body-walls, which are closely applied to the sides. The fore wing is more distinct than the other, its surface being marked by a large squarish dark spot. In contradistinction to these rudimentary organs, the wings and antennæ, the unusual size of the legs is very striking. This extreme development of the legs is rendered necessary in order to enable the insect to move about and deposit its eggs.

Fig. 10. ×7. The outline of the left fore wing of a female pupa of *Orgyia antiqua*. The wing was somewhat flattened.

Fig. 11. ×7. The outline of the left fore wing of a female imago of *Orgyia antiqua*. Here also we meet with proof of recent degeneration; for the imaginal structure is much smaller than the pupal structure within which it develops.

Fig. 12. ×14·5. The male pupa of *Fumea nitidella*, as seen from the left side. The parts shown in the next figure were detached from the pupa. The drawing was made from an empty pupal shell, so that the ventral margin of the fore wing is rolled inwards to some extent. The pupa is well formed, and contrasts in a remarkable manner with that of the female (fig. 14).

Fig. 13. ×14·5. The head, antennæ, and limbs of the male pupa of *Fumea nitidella* represented in the last figure, as seen from the ventral aspect. These parts also are seen to be extremely well developed.

Fig. 14. ×14·5. The female pupa of *Fumea nitidella* as seen from the right side. The difference between the sexes is very marked (compare with figs. 12 and 13). The female pupa is nevertheless far less degenerate than the imago which emerges from it. The imaginal wings are minute tubercles, so that the insect is described as "wingless"; those of the pupa are seen to be small but quite distinct. Their small size leads to the uncovering of the first abdominal spiracle, which is concealed in all pupæ with normally-developed wings. The pupal antennæ are also larger than those of the imago. Although the degeneration of the female *Fumea* is doubtless far older than that of *Orgyia* or *Hybernia*, a comparison between pupa and imago clearly shows that it is not very ancient; for the pupa, although degenerate, is still a long way above the condition to which the imago has sunk.

Fig. 15. ×14·5. The anterior part of the female pupa of an unnamed Psychid, as seen from the ventral aspect and somewhat from the right side. The wings are distinct, although very rudimentary; they are in the form of small pouches. The first abdominal spiracle is uncovered as in fig. 14, and is shown on the right side (left side of figure). The three pairs of thoracic legs and the antennæ (A) are distinct, although very small. The eye (E) is extremely minute, and the mouth-parts are in a very rudimentary condition. The female moth does not emerge from the pupal shell, and is a mere sack full of eggs, bearing no traces of limbs, wings, &c. Nevertheless the pupal prothorax splits in the middle line, and some of the hairs of the included

moth project from the opening (see figure), so that the initial part of the process of emergence is still preserved in this degenerate form. The comparison between pupa and imago confirms the conclusion already arrived at, that the degeneration of female imagines of Lepidoptera is comparatively recent in date. The male pupa of this species is well developed.

Fig. 16. ×7. The left pupal wings of *Cynthia cardui*. The hind wing (H.W.) is seen at two points along the dorsal margin of the fore wing, which covers it elsewhere. Well within the hind margin (H.M.) of the pupal fore wing is seen a hind margin (H′.M′.) which corresponds to that of the imaginal wing. It is clear that the imaginal wing is only developed over a part of the space enclosed by the pupal wing. Thus the venation extends up to the future imaginal hind margin (H′.M′.), and there abruptly ceases (compare fig. 18), while the arrangement of the pigment also undergoes abrupt modification at the same limits. Some traces of the alternation of black and white which is so conspicuous in the fringe of the imaginal hind margin (fig. 17) may also be detected in the disposition of the pigment along H′.M′. In this and the succeeding figures of pupal wings, the cuticle was flattened as far as possible in order to facilitate the drawing.

Fig. 17. Natural size. The outline of the left fore wing of the imago of *Cynthia cardui*, for comparison with the last figure. The hind margin of the wing is seen closely to resemble the corresponding line upon the pupa (H′.M′.), the only difference being that the bay is *slightly* deeper in the imago. A smooth continuous hind margin is far commoner than a bayed or indented margin in Lepidoptera, and is probably more ancestral. It appears therefore that, as in other structural changes of recent date, the pupa presents us with an earlier stage of the process of modification.

Fig. 18. ×7. The left pupal wings of *Vanessa Atalanta*. The venation is remarkably distinct, and the parts which are represented correspond precisely with that of the imaginal wing. This is all the more remarkable because the tracheæ of the pupal wing possess at first an arrangement entirely different from that which they will assume in the imago. The abrupt termination of the veins at H′.M′. is extremely distinct.

Fig. 19. Natural size. The outline of the left fore wing of the imago of *Vanessa Atalanta*, for comparison with the last figure. The position of the dark markings on the fringe is indicated by thickenings. The bay is seen to be somewhat deeper than in the corresponding pupal line (H′.M′. fig. 18).

Fig. 20. ×7. The left pupal wings of *Vanessa Io*. In the dark varieties of this pupa the pigment is distributed along H′.M′. in a manner which suggests a former fringe. The dark parts along the margin are diagrammatically indicated by thickenings, and it is seen that they correspond in number and position with the dark parts of the fringe of the imago of *V. Atalanta* and *C. cardui* (compare figs. 17 and 19). This is all the more remarkable because the imago of *V. Io* does not possess a black-and-white fringe like the other allied forms. Inasmuch as the two former are the more ancestral, as shown by their less indented hind margins, and especially by the arrangement of their markings, it is probable that the condition of the dark pupæ of *V. Io* points towards the former existence of a black-and-white fringe in the imago of this species.

Fig. 21. Natural size. The outline of the left fore wing of the imago of *Vanessa Io*, for comparison with the last figure. The imaginal hind margin is seen to be decidedly more sharply indented than the corresponding part of the pupa (H′.M′. fig. 20).

Fig. 22. ×7. The left pupal fore wing of *Vanessa polychlorus*. The cuticular pigment is represented as accurately as possible. The relation of the pigment and the traces of the venation to the future imaginal hind margin (H′.M′.) are very distinctly shown.

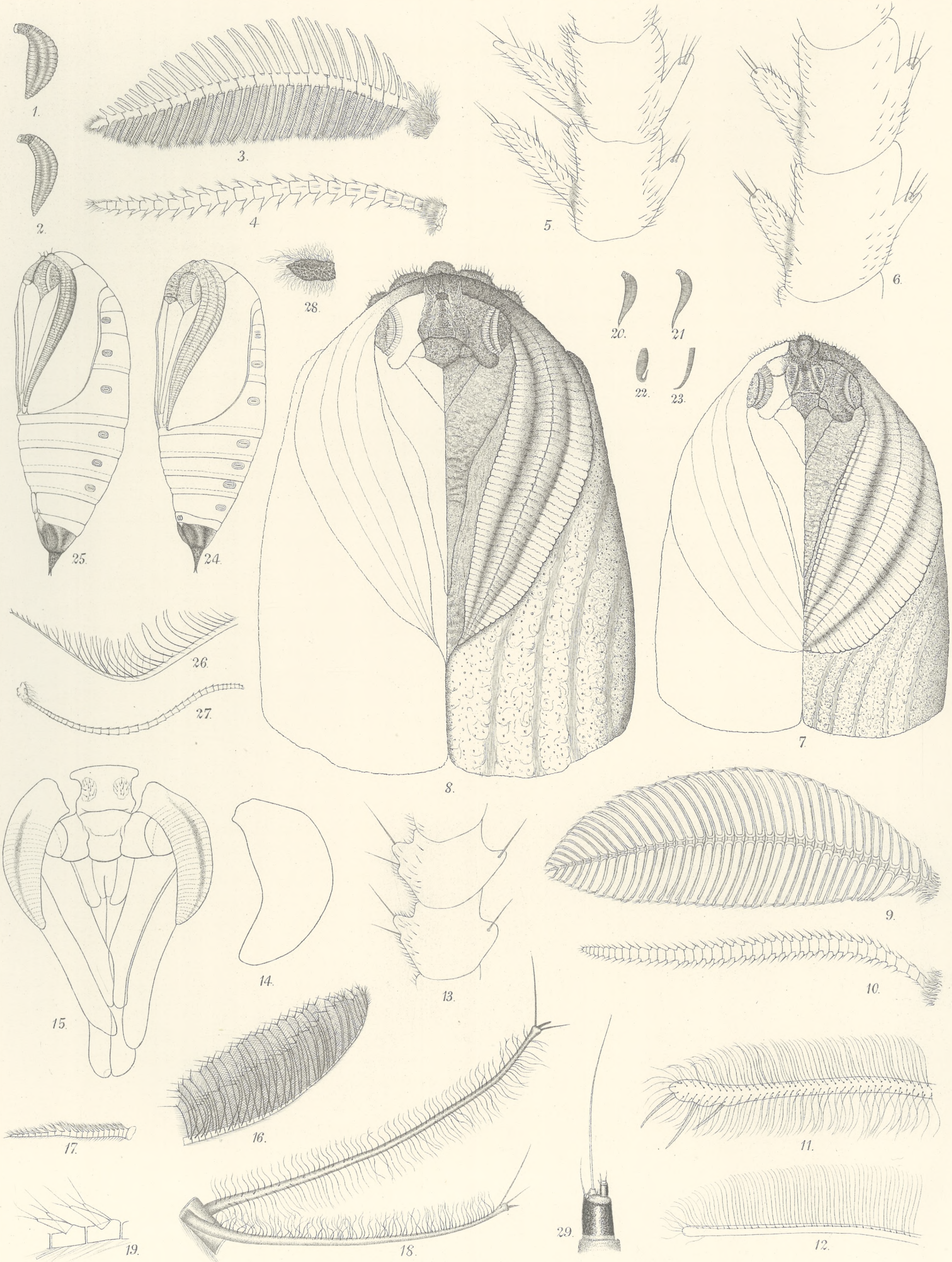
Fig. 23. Natural size. The outline of the left fore wing of the imago of *Vanessa polychlorus*, for comparison with the last figure. The hind margin is seen to be *slightly* more indented than the corresponding line upon the pupa (H′.M′. fig. 22).

Fig. 24. × 7. The left pupal wings and adjacent parts on the dorsal side of *Grapta C-album.* In the previous figures of pupal and imaginal wings (figs. 16–23) the general sequence leads from species with a comparatively simple and continuous hind margin (figs. 16–19) to those with a more indented hind margin (figs. 20–23). The sequence being from more generalized to more specialized and recent types, it was found that the mark representing the imaginal hind margin on the pupal wing, when it differs from the hind margin of the imago, always varies in the direction of greater simplicity. This being the case, I was very anxious to test these results by an examination of the pupal representative of the imaginal hind margin in *Grapta,* which possesses a far more jagged and indented hind margin in the imago than any other species found in this country. The pupal line is shown at H′.M′., and comparison with the corresponding part of the imago (fig. 25) shows at once that a more ancestral condition of the imago is preserved in the pupal sculpture and markings. Fig. 25 shows us a hind margin which is the culmination of specialization in this direction, while the corresponding part of the pupa is not widely different from the condition met with in the imago of *V. polychlorus* (fig. 23) or *V. Io* (fig. 21). The white areas surrounded by pigment on the metathorax and first abdominal segment correspond to two of the golden spots upon the living pupa.

Fig. 25. Natural size. The outline of the left fore wing of the imago of *Grapta C-album,* for comparison with the preceding figure.

Fig. 26. × 7. The arrangement of the main tracheal system in the left hind wing of the pupa of *Papilio Machaon,* as seen from within (viz. corresponding to the underside of the imaginal wing). Comparison with the imaginal wing shows that, although the venation of the latter corresponds in a general way with the arrangement of the pupal tracheæ, the details are widely different. The same facts hold for the fore wing of pupa and imago. We therefore see that the tracheæ of the pupal wings do not by any means follow the arrangement mapped out on the pupal cuticle, an arrangement which they will afterwards assume when enclosed in the veins of the wing of the developing imago.

Trans. Linn. Soc. Ser. 2. Zool. Vol. V. Pl. 26.



E. B. Poulton del. E. Carter sc.

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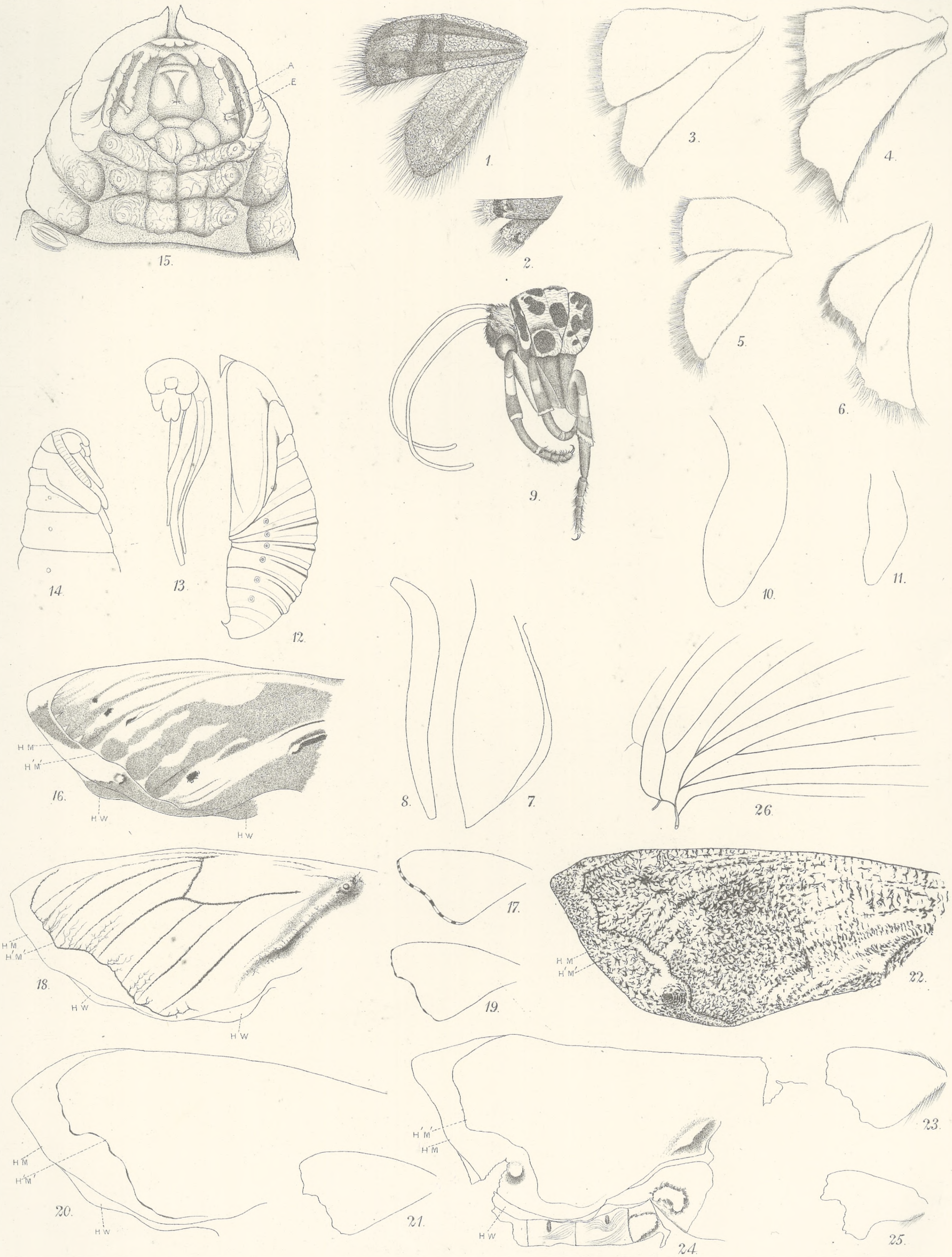
ANTENNÆ OF LEPIDOPTEROUS PUPÆ.



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WINGS OF LEPIDOPTEROUS PUPÆ.

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	Part VI.	1888	0	6	0	0	4	6
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	Part II.	1888	0	5	0	0	3	9
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	Part II.	1882	0	5	0	0	3	9
	Part III.	1883	0	10	0	0	7	6
	Part IV.	1883	0	3	0	0	2	3
	Part V.	1883	0	3	0	0	2	3
	Part VI.	1884	0	13	6	0	10	0
	Part VII.	1884	0	9	6	0	7	0
	Part VIII.	1884	0	10	0	0	7	6
	Part IX.	1886	0	7	0	0	5	0
	Part X.	1887	0	3	4	0	2	6
	Part XI.	1886	0	6	0	0	4	6
	Part XII.	1886	0	8	0	0	6	0
	Part XIII.	1887	1	7	0	1	0	0
	Part XIV.	1887	0	7	0	0	5	0
	Part XV.	1887	0	10	0	0	7	6
	Part XVI.	1888	0	2	6	0	2	0
III.	Part I.	1888	3	12	0	2	14	0
	Part II.	1891	0	5	0	0	3	9