XIII. The Colour-relation between the pupæ of Papilio machaon, Pieris napi and many other species, and the surroundings of the larvæ preparing to pupate, etc. By F. Merrifield, F.E.S., and Edward B. Poulton, M.A., F.R.S., etc., Hope Professor of Zoology in the University of Oxford.

#### [Read October 5th, 1898.]

- A.—INTRODUCTORY. (F. MERRIFIELD and E. B. POULTON.)
- B.-EXPERIMENTS UPON THE PUPÆ OF Papilio machaon.
  - 1. Experiments upon the Summer Pupæ of Papilio machaon. (F. M.)
  - 2. Results of the above Experiments. (E. B. P.)
  - 3. Experiments upon the Winter Pupæ of Papilio machaon. (F. M.)
  - 4. Results of the above Experiments. (E. B. P.)
  - 5. Mr. C. V. A. Peel's Winter Pupæ of Papilio machaon described. (E. B. P.)
- C.—EXPERIMENTS UPON THE PUPÆ OF Papilio podalirius. (Cora B. Sanders and E. B. P.)
- D.—EXPERIMENTS UPON THE PUPÆ OF Pieris napi.
  - 1. Experiments upon the Winter Pupæ of Pieris napi. (F. M.)
  - 2. Results of the above Experiments. (E. B. P.)
- E.—EXPERIMENTS UPON THE PUPÆ OF Pieris brassicæ.
  - 1. Experiments upon the Winter Pupæ of Pieris brassicæ. (F. M.)
  - 2. Results of the above Experiments. (E. B. P.)
  - 3. Experiments upon the Winter Pupæ of Pieris brassicæ. (E. B. P.)
  - 4. Experiments with conflicting colours upon the Winter Pupæ of Pieris brassicæ. (E. B. P.)
- F.—NOTES ON THE STRUGGLE FOR EXISTENCE IN THE LARVÆ OF Pieris brassicæ. (E. B. P.)
- G.—EXPERIMENTS UPON THE PUPÆ OF Pieris rapæ.
  - 1. Experiments upon the Winter Pupæ of Pieris rapæ. (F. M.)
  - 2. Results of the above Experiments. (E. B. P.)
  - TRANS. ENT. SOC. LOND. 1899.—PART IV. (DEC.) 25

#### H.—EXPERIMENTS UPON THE PUPE OF Vanessidæ.

- 1. Experiments upon the Pupæ of Vanessa urticæ and Pyrameis cardui. (C. B. S. and E. B. P.)
- 2. Experiments upon the Pupæ of Vanessa io. (Mabel E. Notley, Florence A. Wright and E. B. P.)
- I.—EXPERIMENTS AND OBSERVATIONS UPON THE SUSCEPTIBILITY OF CERTAIN LEPIDOPTEROUS LARVÆ AND PUPÆ TO THE COLOURS OF THEIR SURROUNDINGS. (A. H. HAMM and E. B. P.)
- K.—OBSERVATIONS ON THE COLOUR-RELATION BETWEEN A COLEOPTEROUS SPECIES (Cleonus sulcirostris) AND ITS SURROUNDINGS. (W. Holland and E. B. P.)
- L.—APPENDIX. THE QUALITY OF LIGHT REFLECTED FROM THE COLOURED AND OTHER BACK-GROUNDS EMPLOYED IN THE EXPERIMENTS RECORDED IN THE PRESENT MEMOIR. (SIR JOHN CONROY, F.R.S., and E. B. P.)

#### A.—INTRODUCTORY.

In Prof. Poulton's paper in the Philosophical Transactions of 1887, vol. 178 B. pp. 311-441, "An Enquiry into the Cause and Extent of a Special Colour-relation between certain exposed Lepidopterous Pupæ and the Surfaces which immediately surround them," he recorded some experiments on the full-fed larvæ of Papilio machaon from which he inferred that this species was not susceptible to the colours of its surroundings, a conclusion which surprised him, having regard to the marked dimorphism of the pupe [the larva not showing any corresponding dimorphism to which the different colours of the pupe could be ascribed, as in the case of the geometrid genus Ephyra (Phil. Trans. l. c. p. 437)], and Prof. Poulton suggested that further experiments should be tried, more especially as he had had only eleven larvæ, of which two died. At the meeting at Cambridge in August last of the International Congress of Zoology M. Bordage of Réunion communicated a paper in which he expressed the opinion that the pupæ of the genus Papilio appeared to have lost any susceptibility to colour which they might at one time have possessed, but Mr. Trimen, your President, gave an instance to the contrary, and expressed the opinion that too few experiments had been made to warrant at present any conclusion on the subject.

Early in July last I happened to mention to Prof. Poulton that I had then a considerable number of larvæ of *P. machaon* which I had received from Germany, and at his suggestion I experimented on some of those I had left at this time, receiving much useful information from him personally as well as from the very full record of his experiments on other species, in the paper above referred to, and in his subsequent paper in the Transactions of this

Society for 1892, pp. 293-487.

The experiments in which different species were employed. The results were in large part displayed and an account given of them at the meeting of this Society on October 5th, 1898 (Proc. Ent. Soc. Lond. 1898, pp. xxx—xxxi). Professor Poulton was at the meeting and also showed the results of some further experiments he had been making in 1898 (Proc. Ent. Soc. l. c. pp. xxxii—xxxii). The same day I suggested to him that it would be useful to arrange the results of my experiments according to the standards of colour which he had already published, and construct fresh standards for the species with which he had experimented but little or not at all. He approved the suggestion and agreed to arrange the results accordingly, and also offered to include the results of the experiments he had recently made.

This memoir accordingly appears in our joint names. The name or initials of the worker who conducted the investigation will appear in the heading of each description. Professor Poulton is responsible for the new standards of comparison and the tabulation of all the pupæ. In arranging the pupæ, he allowed due weight to the description of my results so far as I had made one.

F. MERRIFIELD.

A few brief words are all that are necessary to form my introduction to our joint paper; inasmuch as Mr. Merrifield has fully explained the circumstances under which it came to be written. I was only too pleased to act upon his suggestion, and thus to combine the record of our investigations. It is more convenient in every way that there should be a single complete account instead of two less complete ones. The method adopted of placing the initials of the writer after the title of each Section he has communicated makes our individual responsibility perfectly clear.

A portion of my investigations were carried on jointly with Miss Cora B. Sanders, of Lady Margaret Hall, Oxford. These Sections are preceded by her name or

initials as well as my own.

The experiments upon the colours of the pupæ of Vanessa io were carried on, under my direction, by Miss Mabel E. Notley and Miss Florence A. Wright, of Lady Margaret Hall. Their names are added to the title of the Section in which the experiments are described.

Some interesting observations of Mr. A. H. Hamm and Mr. W. Holland of the Hope Department of Zoology, Oxford, form in large part or entirely the subjects of two

Sections to which their names have been added.

Sir John Conroy, F.R.S., very kindly helped me in determining the quality of the light reflected from the various backgrounds, and his name has been similarly added to the Appendix in which our results are described.

I wish also warmly to thank Mr. W. Holland and Mr. A. H. Hamm of the Hope Department for their most efficient help in many parts of the work; Mr. C. V. A. Peel for kindly lending specimens which have been described, and Mr. Arthur Sidgwick and Mr. Nicholson for drawing my attention to interesting observations made by them which are recorded in Section I.

E. B. POULTON.

# B.—EXPERIMENTS UPON THE PUPÆ OF Papilio machaon.

## 1. Experiments upon the Summer Pupæ of Papilio machaon. (F. M.)

I am generally away from home from nine or ten o'clock until five or later, and therefore my opportunities for taking a larva just at the right moment, when it has done feeding and before its sensitiveness to colour has begun, are imperfect. But I was able to select fourteen larvæ, which seemed to have arrived at the full-fed stage, and I prepared a few glass cylinders of about 6 inches in height and mostly  $3\frac{1}{4}$  inches in diameter, though some were an inch or two wider, which I placed in flower-pots nearly filled with earth. They were in two divisions, viz. (1) furnished with dark sticks, and (2) furnished with light sticks. Division (1) had about six dark brown sticks of from  $\frac{1}{4}$  to  $\frac{2}{8}$  of an inch in diameter taken from an old

faggot-stack, and had a roof of black net. Division (2) had the same number of peeled and therefore nearly white willow slips of the same size, and had a roof of white muslin. The sticks were secured by driving them into the earth, and the cylinders were in both cases exposed to the same amount of light, i. e. close to a rather large window, but on most days moved from the W.N.W. to the E.S.E. side of the house, and back, to avoid hot sunshine. As larvæ, where crowded, have been found to affect each other's pupal colouring (Phil. Trans. 1887, l. c. Ent. Trans. 1892, l. c.), only two or three were placed in each cylinder.

I exhibit the eleven pupæ or pupa-cases, which were obtained under these conditions. As the dark pigment resides in the pupa-case, it is easy to see on examining this whether the pupa was a green one or not, as, if the pupa was a green one, the pupa-case is practically free from pigment, though sometimes stained in places by the meconium, whereas if the pupa was bone-coloured the case

It was obviously desirable to ascertain what was the proportion of grey \* and yellow-green pupæ in my stock, and on going through the whole remainder of them, 145 in number, I found that 76 might be described as of the former and 69 of the latter or yellow-green form. Many of these however were of intermediate colouring, and it was not easy to classify them. Seven of the 145 had pupated on the green carrot-tops on which the larvæ had been fed; of these six were yellow-green, one was grey.

This made a very strong case for susceptibility, but it was not conclusive, and I determined to try the experiment

on a larger scale with the second brood.

Before describing in detail the results of this and other experiments it is necessary to tabulate the colours which the pupa of *P. machaon* is known to assume, so as to have a standard of comparison. The following table and description were made by Prof. Poulton on May 2nd, 1899, after carefully comparing the whole of my pupæ together with a number belonging to Mr. C. V. A. Peel.

2. RESULTS OF THE ABOVE EXPERIMENTS. (E. B. P.)

There is a distinct dimorphism in the pupæ of Papilio machaon, and the intermediate forms are very rare as

<sup>\*</sup> See note on page 374.

compared with the extreme. The two forms may be classified as (1) yellow-green, and (2) grey.\* The former have a yellow ground-colour with deep green markings, the latter a bone-coloured ground with dark purplish brown, and in places black markings. With few exceptions the dark markings of the grey forms correspond in position with the green markings of the yellow-green forms, the chief exceptions being on the surface of the pupal wings, where the green forms a more continuous area, less interrupted by the yellow ground-colour than the dark

marking is by bone-colour.

This correspondence in position becomes all the more interesting and remarkable when it is remembered that the two markings are entirely different in constitution, origin, and even in the pupal layers in which they are respectively situated, the green pigment being relatively unstable, probably a modified form of chlorophyll derived from the food-plant, and situated in the deeper laminated layers of the pupal cuticle, the dark pigment being very stable (remaining permanently in the empty pupal case), solely due to the metabolic activity of the animal organism, and confined to the thick layer of cuticle which lies above the laminated layer and forms the outermost part of the pupal shell. (See Poulton, Proc. Roy. Soc. 1885, Vol. xxxviii, p. 279, in which however the laminated layer is erroneously distinguished from the "true cuticle.")

We can again classify the (1) yellow-green and (2) grey

forms as (a) dark and (b) light, thus:—

1. Yellow-green 
$$\left\{ egin{array}{ll} a. & Light & forms. \\ b. & Dark & ,, \end{array} \right.$$
2.  $Grey \qquad \left\{ egin{array}{ll} a. & Light & ,, \\ b. & Dark & ,, \end{array} \right.$ 

<sup>\*</sup> I formerly spoke of the darker pupæ as brown (Phil. Trans. 1887, l. c. p. 407), a description which is clearly incorrect. Mr. Merrifield has introduced the appropriate term "bone-coloured," which accurately expresses the appearance of the ground-colour of these pupæ as well as those of the corresponding forms of Pieris napi and P. rapæ. The whole appearance of these pupæ is however due to the combined impression made by the pale ground-colour and the dark markings, and I think that "grey" expresses this effect as a whole more truly than any other word; although there are pupæ in which the markings are so inconspicuous that the effect seen is that of the ground-colour alone.

A light yellow-green form (1 a) is bright yellow over the dorsal surface slightly mottled with green on the sides, this colour becoming distinct round the spiracles and forming a spiracular streak interrupted between the abdominal segments. At the posterior extremity of the pupa this green streak is continued on to the sides of the anal spine, and in the more strongly marked pupe of this degree the whole of the spine is green. The green mottlings are rather more distinct upon the abdominal segments below the spiracular band than they are above it, and have a more pronounced longitudinal arrangement. The dorsal region of the thorax is also more or less mottled with green which becomes concentrated to form a distinct apical patch on the mesothoracic median spine. The wings, limbs, antennæ, and head are deep green, the latter being, in the palest pupe, the most strongly coloured part of the whole surface.

In the more deeply coloured of the light forms (1 a) the mottled green tends to spread backwards from the mesothoracic spine forming a broad indistinct greenish band.

In the dark yellow-green pupe (1 b), further development and coalescence of the mottlings transform this dorsal band into deep green. It occupies the whole dorsal area between the subdorsal rows of small tubercles. Below, the green of the spiracular stripe,—continuous in pupe of this degree —spreads upwards and invades the yellow ground-colour leaving only a yellow lateral band, sharply defined above where it terminates at the level of the subdorsal tubercles, while below it gradually passes into the invading green. Anteriorly this yellow band terminates below the mesothoracic spine. The dorsal green band is palest (yellowest) in its median part and in the posterior half of its length, in front of the caudal spine, the dorsal surface of which is green. The band is also interrupted in the region of the metathorax by a yellow patch, traversed by a green median line.

The light grey forms (2 a) resemble the light yellowgreen (1 a), substituting bone-colour for yellow, and dark purplish-brown for green, allowing of course for the greater contrast between ground-colour and marking which is thus brought about, and for the difference over the wings which has been already alluded to.

The dark grey forms (2 b), by making a similar substitu-

tion, resemble the dark yellow-green (1 b). The purplishbrown is increased in extent as is the green of the corresponding form (1 b), the dark dorsal band becoming a specially prominent feature which contrasts strongly with the appearance presented by the *light grey* pupæ

 $(2 \ a)$ .

I will now apply the arrangement suggested above to the results of Mr. Merrifield's experiment. The pupæ were compared on May 2nd, 1899. Three of the 14 larvæ died without pupating. Of the remaining 11, 6 had been placed in the cylinders furnished with dark sticks; 5 of these pupated on the dark sticks. In comparing these summer pupæ and putting each in its place in the scale of colour, great assistance was derived from Mr. Merrifield's descriptions made in 1898, when more of the pupæ were alive and those which were dead had changed less extensively.

All the pupe attached to dark sticks were clearly grey forms (1), except one (probably dead), which was intermediate between yellow-green and grey, having a bone-coloured ground with many of the markings, especially upon the wings, greenish instead of brown. Of the remaining 4 pupe, 1 had emerged in 1898, and was intermediate between dark and light grey (2 a, b) or a lightish dark grey (2 b); 1, still alive, was also a (2 a, b); 2, dead, were

certainly grey, and probably dark grey (2 b).

The sixth pupa was dead and much discoloured, but from Mr. Merrifield's description in 1898, it had evidently been a yellow-green form (1 a) or (1 b): "The larva had imperfectly attached itself to a dark stick and had then, before pupating, fallen on the earth which, being moist, was of a dark colour. It had there formed a yellow-green pupa, somewhat misshapen."

Of the 5 placed in light surroundings, 4 were attached

to shaved white sticks.

Two were dead, but both were evidently yellow-green, one probably a light and the other a dark form of this degree,  $(1 \ a)$  and  $(1 \ b)$ .

Two had emerged, but both had been yellow-green and one certainly a light form  $(1 \ a)$ , the other probably dark

(1 b).

The fifth pupa, attached to the white muslin top, had also emerged. This pupa was an exception, being a distinct light grey form (2 a).

## 3. Experiments upon the Winter Pupæ of Papilio machaon. (F. M.)

In order to continue the experiments, begun upon the summer pupæ, I obtained from Germany, from the 31st of August to the 2nd of September, 1898, about 150 more larvæ, most of them young.

Apparatus.

In order to cope to some extent with the difficulty I had in taking the larvæ just at the right moment, owing to my long daily absences from home, I provided two special breeding-cages. These were made of  $\frac{5}{16}$  inch deal, each in two compartments. Thus there were four compartments the external dimensions of which were 16 inches in height, 12 inches in depth from front to back, and 8 inches in width. The front of each cage was a sheet of glass, about 14 inches in width and 12 inches in height, as it started at 3 inches from the bottom; it was vertically divided down the middle by the thin deal partition between the two compartments. The backs were of perforated zinc, corresponding in size with the glass fronts, and the outer sides were of deal containing the doors. The tops were open, but covered with woven material as stated below. framework of the top, and generally, was about an inch wide, and there were many angles more or less shady, vertical, and horizontal, where the parts of the framework met at right angles.

The whole of the interior, except the glass front and the perforated zinc backs, was covered with tissue-paper; black in the black compartment, white in the white compartment, green in the green compartment, and about one-half orange and one-half yellow (the division being vertical) in the orange-yellow compartment. The perforated zinc backs and the open tops were covered with woven material, viz. the black compartment with double black muslin (covered with a slate), the white compartment with double white calico, the green compartment with threefold yellow-green art muslin (fourfold on the top except for the brassicæ experiment hereafter described when it was twofold), the orange-yellow compartment with orange-yellow leno; this leno, instead of paper, being also used in some of the angles of

the framework.

The fronts of the cages were placed within a few inches

of a second-floor window about 3 feet wide and 6 feet high, they were facing the W.N.W. and looking into an open country, and were often screened by a muslin window-blind during hot sunshine. No direct light from the sky reached any part of the interior except a small part of the bottom and of the sides.

Much orange light came through the roof of the first compartment, very little greenish light through the top of the green compartment, and much white light through the top of the white compartment; in addition to white direct light, much was reflected from the coloured interior of these three compartments, but the black compartment was very dark inside except the part close to the glass front.

The effect was that the black compartment was for the most part very dark; the white, green and orange-yellow compartments much lighter, as the tops transmitted much light, and the colours were such as to reflect a great deal In the green compartment, however, while covered with the fourfold art muslin, very little light came through the top. In all cases a little light came in through the chinks of the doors, and a very little through the draped perforated zinc at the back. In all four compartments there were shady regions in the angles of the framework, and I found so many of the larvæ had a disposition to select these shadier regions for pupating, where of course the coloured light would operate less strongly, that I found it expedient to transfer them, when I could do so in time, to receptacles where they were exposed to stronger light. For these purposes I prepared glass cylinders of the dimensions before mentioned, covered at the bottom and for about two-thirds of the outside circumference with paper of the appropriate colour, leaving clear the one-third next the window, and the tops being usually covered with paper of the same colour, but sometimes with clear glass. In this way I fitted up cylinders for the following colours: black, white, green, yellow, orange, Dutch "gold," all provided with sticks covered with paper of the corresponding colour. These cylinders were placed on thin pieces of wood or cork carpet with tintacks driven through the bottom, forming spikes on which the coloured sticks were fixed. The bottoms, as well as about two-thirds of the circumference opposite the light, and the tops, were covered with single or double paper of the proper colour

secured by three ties of thread and on the tops by a sheet of clear glass. In the case however of the dark sticks the bottom was of dark cork carpet, and these cylinders were clear all round, with a sheet of clear glass on the top.

In order not to crowd the larvæ, it was my practice to transfer them, when spun up on the sticks, to wide-mouthed Bordeaux plum-bottles of clear glass having a greenish hue, of about the same size as the cylinders, but fitted for two-thirds of their circumference with coloured paper inside instead of outside, and I sometimes transferred larvæ direct from the compartments of the breeding-cage to these bottles, as pupating against glass in front of coloured paper did not appear to me to be the same thing in effect as pupating against the coloured paper. In these bottles the coloured paper was inside, and therefore nearer the larvæ than in the cylinders. The sticks in the bottles could not be prevented from shifting as heavy larvæ crawled over them, and the larvæ appeared to dislike this, and to be more restless and slower in pupating than when the sticks were fixed.

The cylinders and bottles were placed within a few inches of the window above referred to, or of another window having the same aspect, but only about 4 feet high by 3 feet wide. As the objects in both were necessarily near the light, and, except in those given over to black, light, coloured or uncoloured, was admitted all round and by the tops, the larvæ in these were as a rule exposed to much more light, both direct and reflected, than those in the breeding-cages.

I also lined a clear glass saucer with green carrot-tops and placed it in a second saucer with green carrot-tops, among which some larvæ pupated, the surface being covered

with a sheet of clear glass.

Most of the machaon larvæ in the cylinders or bottles spun up against the coloured sticks provided for them, but in a few cases they spun either against the glass where it was covered outside by coloured paper or against the clear glass front of the cylinder or bottle. In these cases I always classified the pupæ as "orange through glass" or as "orange on glass," the pupæ in the latter case being often not near the special colour, although the larvæ in moving about had probably been at times exposed to the colour influence. If, however, these larvæ follow the same laws as those of Vanessa urticæ, they are only sensitive when

at rest on the surface upon which they will afterwards pupate. (Phil. Trans. 1887, l.c.) Allowance must be made, on the other hand, for the possible disturbance of larvæ after they have entered the susceptible phase.

#### Colours of the different surroundings.

Besides these black or coloured cylinders or bottles I had clear glass cylinders or bottles supplied with the other objects enumerated below for the pupæ to attach themselves to, some also being shut up in absolute darkness. The result was that I obtained several classes of pupæ, viz. from—

- 1. Black paper (a) in strong light, (b) in more or less shade.
- 2. Dark sticks from old faggots or freshly-cut dark alder.
- 3. Dirty white paint, being that of a breeding-cage ten years old.
  - 4. Darkness.
- 5. Light-coloured dry stems (dead stems of *Epilobium hirsutum*).
  - 6. Dead reeds, light brown in colour.
  - 7. Dull green reeds.
  - 8. Bright golden yellow oatstraw.
  - 9. Dutch "gold," with embossed pattern.
- 10. Green paper (a) in strong light, (b) in more or less shade.
  - 11. Green carrot-tops.
- 12. White paper (a) in strong light, (b) in more or less shade.
- 13. Yellow paper (a) in strong light, (b) in more or less shade.
- 14. Yellow orange leno (a) in strong light, (b) in shady corner.
- 15. Orange paper (a) in strong light, (b) in shady corner.

Some of these had the further differences which are indicated in the exhibit and described in the classification of the pupæ.

I exhibit the results of all these exposures, 72 individuals. All of these may repay study; the details will be described by Prof. Poulton. I could perhaps have made the Exhibition Case more attractive as well as more effective for purposes of comparison had I detached the pupæ from the

coloured backgrounds that in most cases adhered to them; but I thought it eminently desirable that the exhibition should supply its own evidence, so as to enable all who see it to draw, independently, their own conclusions. I supplement it, however, with all the other pupæ obtained in the course of my experiments. As general results it will be enough perhaps here to say that the 16 pupe of P. machaon on the black paper-covered sticks and on dark natural sticks are all grey, with the exception of one, which is yellow-green; those that were in a strong light are very dark; that of the 4 on carrot-tops all are yellow-green; that of the 9 on white paper 1 is grey and the other 8 all yellow-green or light grey with a greenish tinge; that of the 6 on yellow paper 2 are greenish-grey and the other 4 yellow-green; and that of the 4 on orange paper all are yellow-green.

These results seem to me clearly to prove the susceptibility

of P. machaon.

The pupæ of P. machaon on the other coloured surroundings employed did not give such definite results; particulars are given in the next section.

#### (E. B. P.) 4. RESULTS OF THE ABOVE EXPERIMENTS.

The pupæ were compared May 2nd, 1899.

The various conditions to which the larvæ of P. machaon were subjected will be considered in the same order as that adopted by Mr. Merrifield on p. 380.

### (1) BLACK PAPER. (a) In strong light.

2 pupæ, fixed to black tissue-paper, were very dark grey (2 b).

1 pupa, fixed to black tissue-paper, was intermediate

between dark and light grey (2 a, b).

1 pupa, fixed to black tissue-paper, had emerged, and was grey, probably similar to the last.

I pupa, fixed to black net, was dead, and was grey, probably similar to the last.

5

### (b) In fair light.

The single pupa (dead and discoloured) was fixed to black net. It was impossible to place it with any certainty, but the appearance suggested that it had been yellowgreen.

#### (c) In a dark corner.

All the pupæ were fixed to the black paper.

1 pupa was very dark grey (2b).

3 pupæ (one dead) were grey, probably light (2 a).

I pupa was grey, probably intermediate between dark and light (2 a, b).

5

#### (2) DARK STICKS (ONE MUCH LIGHTER THAN THE REST).

All the pupæ were attached to the sticks.

2 pupæ were dark grey, (2 b) one very dark.

1 pupa, on the lightest bark, was light grey (2 a).

2 pupæ (dead) were grey, probably light (2 a).

1 pupa (dead) and much altered, was probably the yellow-green form (1) described by Mr. Merrifield on p. 381.

6

#### (3) DIRTY WHITE PAINT.

1 pupa, fixed to the painted surface, was intermediate between dark and light grey (2 a, b), but with some tendency, in the possession of a greenish tinge, towards the yellow-green form (1).

1 pupa, fixed to the painted surface, was dead and changed in colour, but it had probably been

yellow-green (1).

2

#### (4) DARKNESS.

2 pupæ were intermediate between dark and light yellow-green (1 a, b).

1 pupa (dead) had altered in colour, but had been a light form of either (1) or (2).

1 pupa was probably *light yellow-green* (1 a), but had darkened, apparently preparatory to emergence.

1 pupa was intermediate between (1) and (2) and also intermediate between dark and light (a, b).

5

The absence of strong pigmentation, and the tendency towards yellow-green rather than grey, were the marked results of darkness, so far as these 5 pupæ are concerned.

#### (5) LIGHT-COLOURED DRY STEMS (Epilobium hirsutum).

1 pupa (dead and discoloured) was probably *light grey* (2 a).

1 pupa (dead, or perhaps discoloured, preparatory to emergence) was probably a *yellow-green* form (1).

2

#### (6) DEAD, LIGHT BROWN REEDS.

Both pupe had become greatly discoloured, and one at least was dead. The position of one was uncertain; the other had apparently been a *yellow-green* form (1).

#### (7) DULL GREEN REEDS.

1 pupa, fixed to reed, was intermediate between dark and  $light\ grey\ (2\ a,b)$ .

1 pupa, fixed to reed, was intermediate between grey

and yellow-green (1, 2).

(8) OATSTRAW (BRIGHT GOLDEN YELLOW).

1 pupa, fixed to straw, was a light grey form (2 a), with

some tendency towards yellow-green.

1 pupa, fixed to straw (dead and discoloured) was of uncertain position, but clearly it had not been highly pigmented.

2

#### (9) DUTCH "GOLD" (EMBOSSED).

1 pupa, fixed to "gold," was intermediate between dark and light grey (2 a, b), with a slight tendency towards the yellow-green form (1).

1 pupa, fixed to "gold" (dead), was intermediate between dark and light yellow-green (1 a, b).

2

#### (10) GREEN PAPER. (a) In strong light.

1 pupa was dark yellow-green (1 b).

1 pupa was light grey (2 a).

1 pupa was dead and of uncertain position, but probably it had never been strongly pigmented.

#### (b) In good light.

The single pupa was dead and discoloured, and its position uncertain. It was obvious however that it had not been strongly pigmented.

#### (c) In fair light.

1 pupa was intermediate between light yellow-green and light grey (1 a, 2 a).

1 pupa (dead or emerging) was probably a yellowgreen form (1).

2

#### (d) In shady corner.

1 pupa was light grey (2 a).

1 pupa was intermediate between light and dark grey (2a, b).

2

#### (e) Fixed to glass near the green paper.

The single pupa was dead, and so discoloured that it

could not be placed.

Hence green paper is far less powerful than yellow or orange paper (Nos. 13, 14, 15), or the natural green of chlorophyll (No. 11) in the production of green pupæ of this species, thus agreeing with the results already obtained in the case of other species (Phil. Trans. 1887, and Trans. Ent. Soc. 1892, l. c.). It is noteworthy that the most shaded part of the green surface produced the strongest tendency towards grey forms.

#### (11) GREEN CARROT-TOPS.

1 pupa was intermediate between dark and light yellow-green (1 a, b).

3 pupe (dead or emerging) were yellow-green, probably of the same shade as the above  $(1 \ a, b)$ .

4

#### (12) WHITE PAPER. (a) In strong light.

4 pupe were *light yellow-green* (1 a), one of them with a tendency towards grey (2), and one very remarkable in possessing an almost white ground.

1 pupa was intermediate between light and dark yellow-green (1 a, b).

1 pupa was discoloured, but had probably been intermediate between a light and dark grey (2 a, b).

6

The form with white ground perhaps indicates some special influence of the surroundings in the direction of producing a peculiarly close resemblance; but more experiments are needed in order to render it certain that the case was not that of a rare individual peculiarity.

#### (b) In fair light.

1 pupa was intermediate between light and dark yellow-green (1 a, b).

1 pupa was light yellow-green (1 a), with a tendency

towards bone-colour in the ground (2).

2

#### (c) In dark corner.

The single pupa was discoloured, but was probably light yellow-green  $(1 \ a)$ , with some tendency towards grey (2).

#### (13) YELLOW PAPER. (a) In strong light.

1 pupa was dark yellow-green (1 b).

3 pupe were yellow-green (1), discoloured, but probably light (1 a), or intermediate between light and dark (1 a, b).

2 pupæ were light yellow-green (1 a), with some

tendency towards grey.

6

#### (b) Through glass.

The single pupa was dead, and had entirely blackened.

#### (c) On glass.

The single pupa was discoloured, but was probably yellow-green, and certainly had not been highly pigmented.

#### (14) YELLOW-ORANGE LENO.

This label could not be found as distinct from the yellow (13) and orange (14); or I may have overlooked it. The results are certainly included in one or more of the sub-divisions of (13) or (14), inasmuch as the total number of the pupæ examined is 72,—the number given by Mr. Merrifield.

TRANS. ENT. SOC. LOND. 1899.—PART IV. (DEC.) 26

(15) ORANGE PAPER. (a) In strong light.

3 pupæ were light yellow-green (1 a).

1 pupa was dark yellow-green (1 b).

4

#### (b) Through glass.

The single pupa was dead or emerging, but appeared to have been intermediate between dark and light grey (2 a, b).

(c) In shady corner.

2 pupæ were light yellow-green (1 a).

1 pupa was light grey (2 a).

3

As Mr. Merrifield has stated on p. 381, the examination of these pupæ seems "clearly to prove the susceptibility of P. machaon." At the same time there was one unsatisfactory point in the evidence, viz. the extremely unhealthy condition of the pupæ. A large solitary ichneumon began to emerge from the pupæ in the autumn of 1898, soon after the date at which Mr. Merrifield showed them before this Society (October 5th, 1898). At intervals they continued to emerge until the early summer; and soon after my examination was made on May 2nd, 1899, they came out suddenly in large numbers. The ichneumons almost invariably gnawed a hole in the pupal wing, in order to escape. The whole batch produced very few butterflies.

It was unfortunate that press of work prevented me from comparing the pupæ until so late, when the discoloration of many of them had proceeded so far; but under any circumstances it was much to be desired that the susceptibility of undoubtedly healthy pupæ should be tested. Such a test I have fortunately been able to apply, and the result confirms Mr. Merrifield's conclusion in the most complete and convincing manner, as may be seen from the succeeding section.

### 5. Mr. C. V. A. Peel's Winter Pupæ of Papilio machaon described. (E. B. P.)

Through the kindness of Mr. Peel I have been able to compare a fine set of very healthy pupæ from Wicken Fen. The pupæ were in part attached to green reeds; in

part to the wood (somewhat darkened by age), and in part to the perforated zinc of two ordinary rectangular breeding-cages. It is clear that the two latter sets of pupæ had been formed from captured larvæ, while the set attached to reeds may have been, in part at least, found so attached in the open. Mr. Peel is not sure upon the point; but the fact that reeds, and reeds only, have been selected is in favour of this interpretation. The majority of the pupæ have now emerged successfully, and nearly all of those that remain are still healthy. Very few have The entire absence of parasites in this set of larvæ, as compared with their excessive abundance in Mr. Merrifield's continental individuals is of high interest, and suggests the same conclusion as that at which I arrived last year in breeding large numbers of Continental and English larvæ of Vanessa urticæ, viz. that the greater abundance of birds in this country may, by destroying parasites, compensate for their direct attacks on the species of Lepidoptera (see Report of British Association, 1898, Section D). I will now give the results of the examination which was made on May 3rd, 1899.

#### 14 pupæ attached to reeds.

Thirteen pupe were distinct light yellow-green (1 a). Of these 2 were fixed at some distance from each other on the same reed, while 10 were on separate reeds. Just below the thirteenth pupa was fixed the single exception a dark grey pupa (2 b).

#### 19 pupæ upon wood or zinc.

In the breeding-cage which contained the reeds, one  $dark\ grey\ (2\ b)$  pupa was lying loose upon the floor, and another of the same kind  $(2\ b)$  was attached to the zinc.

In another breeding-cage 5 pupæ were attached to the zinc, in a curved line, near together. From above downwards their arrangement was—

2 pupæ intermediate between dark and light grey (2 a, b).

1 pupa dark grey (2 b).

1 ,, again intermediate (2 a, b).

1 ,, light grey (2 a).

Thus the central pupa was darkest, as though some influence had been exerted by the neighbouring larvæ or pupæ (as is so markedly the case in *Vanessa*).

Above these 5 pupe, on the wooden roof, were 3 pupe, two close together and one near them in the corner. All were light grey (2 a).

At the opposite end of the cage 3 pupæ were scattered over the zinc, one being intermediate between dark and

light grey (2 a, b), two, dark grey (2 b).

On the wooden roof over them was a compact group of 5 pupe, all intermediate between dark and light grey  $(2 \ a, b)$ ; while a single pupa loose on the floor was also

intermediate (2 a, b).

Thus there was not a single exception among the pupæ on the zinc and wood. Furthermore those fixed to the latter were on the whole lighter than those fixed to the darker zinc. The singular completeness of the result is best shown in a tabular form as follows:—

	Yellow-g	green (1)	Grey (2)					
	Light (a)	Dark (b)	Light	(a)	Da			
Attached to green reeds	13	-	-		1		=14	
			In	term	edia	ite.		
Attached to wood of cage	_	_	3	5		_	= 8	
Lying loose on wooden floor (more in shade than roof and sides, and with dark débris scattered over it)	_	_	_	1		1	= 2	
Attached to zinc	_	_	1	4		4	= 9	

It is unnecessary to examine these data further. It is obvious on an inspection of the above table that there is only a single exception to the complete susceptibility

of the pupæ.

The much greater susceptibility of this set of pupæ as compared with Mr. Merrifield's considered as a whole, and with the few upon which I experimented in 1886 (Phil. Trans. 1887, l. c. p. 406), is probably due to their more healthy and vigorous condition, and perhaps in part to some of the results having been obtained under normal conditions (if it is admitted that most of the green pupæ were formed in the open). The larvæ are not gregarious, so there is no justification for assuming a family tendency towards susceptibility on the part of the set as a whole.

Local differences in susceptibility are of course possible, and an enquiry directed along this line might lead to

results of high interest.

It is a great pleasure to me to see this species, upon which so much doubt has been thrown—in the first place in the discussion which followed Mr. T. W. Wood's communication to this Society in 1867 (Proc. pp. xcix—ci), and nineteen years later as the results of my experiments—now finally proved beyond doubt to be susceptible to the colours of its environment. This result, which we owe to Mr. Merrifield, is a further warning against the errors into which we are liable to be led by relying, as Mr. Bond did (in the 1867 discussion), upon a general impression gathered from a wide experience not specially directed towards the solution of the problem, as I did, upon an insufficient number of individuals subjected to experiment.

# C.—EXPERIMENTS UPON THE PUPÆ OF Papilio podalirius. (Cora B. Sanders and E. B. P.)

Five full-fed larvæ of this species were found by us in Switzerland, between Visp and Stalden, on July 22nd, 1898. They were all, except one, of the usual yellowstriped green form. The single exception was brownishgreen with many red spots somewhat similar to those which occur upon certain forms of the larvæ of Smerinthus ocellatus and S. populi. It is possible that the darkened ground colour was due to changes preparatory to pupation, or perhaps to ill-health, as the larva died without pupating. Two of the larvæ were placed in a white muslin bag and offered green reeds together with the green twigs and leaves of the food-plant: three were placed in a black net bag, and provided with dark brown branches, as well as the food-plant. In a few days four of them pupated, one being fixed to the white muslin and three to the black net.

It was immediately seen that the latter were far darker than the former. A careful comparison was made on

May 3rd, 1899.

The pupa which had been fixed to white muslin was a pale dull orange tint, especially dull over the wings. Of the other three which had been fixed to black net, one was also dull orange but of a distinctly darker shade, while the remaining two were much darker still, being of

a purplish-brown deepest in tint over the wings.

These small numbers are not sufficient to prove the susceptibility of this species; but they render such susceptibility probable. It is to be hoped that larger and more varied experiments will be made by those who have the opportunity of obtaining considerable numbers of the larvæ of *P. podalirius*.

## D.—EXPERIMENTS UPON THE PUPÆ OF Pieris napi.

## 1. Experiments upon the Winter Pupæ of Pieris napi. (F. M.)

I exhibited to this Society on November 2nd, 1892 (Proceedings 1892, p. xxx), some pupæ of P. napi showing that the species was susceptible. In this present year I was experimenting on the species for other purposes, and determined to avail myself of the apparatus I had to provide for experiments on the coloration of pupæ of P. machaon. Mr. Harwood supplied me in the early part of August with a number of females captured in the vicinity of Colchester, and from them I obtained several hundred eggs on watercress, on which I fed the larvæ till about their last stage when that food was largely supplemented and finally replaced by cabbage. These when approaching pupation were exposed to the same colour influences as the machaon larvæ had been (substituting green cabbage-leaves for carrot-tops), and to the following in addition (16) planed deal in shade, (17) planed deal in light.

They seemed very unwilling to pupate on orange (except on the glass in front of the orange paper), so I shut up some in (18) a threefold yellow-orange leno cylindrical bag with single leno on the top, and orange paper outside two-thirds of the circumference, and here

they were obliged to pupate.

In this species and in *P. brassicæ* my results are too numerous for me to show the whole in the Exhibition Case; but I have brought with me in glass-bottomed boxes, so that they can be seen, all the pupæ of both species which are not thus displayed (in the Exhibition Case), duly classified. There are in all about 340 pupæ of *P. napi*.

About 80 of the napi not in the general Exhibition Case are in a second Exhibition Case under the following circumstances. I had an old breeding-cage (somewhat resembling those previously described, but a little smaller) in two compartments with a glass roof over both; one of these was lined with black and had its glass top covered with double black tissue-paper, nearly opaque; the other was lined partly with orange paper, and partly with yellow paper or yellow-orange leno, and the glass top was covered with threefold orange leno, transmitting much orange light. Finding that a number pupated on the glass roof, I succeeded in detaching the plate of glass from the roof and mounting it for exhibition in a second case. It will be seen that on the black side there are 34 pupæ all bone-coloured and nearly all much spotted with dark; on the orange yellow side 46 pupæ, all green except 4 which are bone-coloured, though with a yellowish tinge, and nearly all the 46 practically unspotted.

I think this second Exhibition Case, in which the pupæ have arranged themselves, affords a very effective demon-

stration of the sensitiveness of this species.

The following section will contain a detailed statement of results by Prof. Poulton. Here it will be sufficient in reference to the first Exhibition Case to point to the contrast between the 10 on black paper or the 8 on black or dark sticks, all of which are dusky, with much black spotting, and the 19 on yellow or orange paper all of which, with one exception, are green, to the 12 on or near cabbage-leaves, many being attached to the glass bottle, most of which are green, and to the varying colour of those in darkness; the 8 on Dutch gold, the 7 on planed deal, the 8 on green and the 6 on white paper being nearly all bone-coloured, and most of them spotless or nearly so. These results clearly prove the high susceptibility of the pupa.

All the four species experimented on by me, in preparing to pupate vary in colour according to their surroundings, and I do not see any room to doubt, when the 16 pupæ of machaon on black paper or dark sticks are compared with the 4 on green carrot-tops, or when the 18 pupæ of napi on black paper or dark sticks are compared with the 12 which pupated on or near cabbage-leaves, that the adaptation must be in many cases

protective.

#### 2. Results of the above Experiments. (E. B. P.)

The pupe of *Pieris napi* were compared on January 2nd, 1899, with a view to the construction of a standard table.

As compared with the allied P. rapæ, the dimorphism of the ground-colour is far more marked. Furthermore, the ground is almost invariably restricted to bone-colour or green in P. napi, whereas many different shades are common in P. rapæ. Even in pupæ with the darkest markings the bone-coloured ground is far less obscured by generally distributed pigment in napi than it is in rapæ. There is also in the former a marked dimorphism in the arrangement of the black markings, which show characteristic differences even when present in similar amounts in the two forms—bone-coloured and green. Thus the bonecoloured forms, however pale, almost always possess a distinct black patch (made up of two or three spots or short lines) in the centre of the fore wing. This character, which I call the "wing-mark," is either wanting or far less developed in the green forms, even when richly pigmented in other parts of the surface.

Another difference is the far greater irritability of the pupæ of P. napi. A slight stimulus, such as light breath, would almost always cause active movements, when the more stolid pupe of P. rapæ remained quiescent. observation, which certainly held at the time the examination was made, may perhaps have been due to differences in the degree of development then reached by the two

species.

The forms of the two pupæ are almost alike, and as each varies considerably, it is very difficult to distinguish them with certainty by this means; but the above-mentioned tests enabled me easily to pick out two pupæ of P. rapæ, which had found their place among Mr. Merrifield's numerous napi, having been accidentally introduced as larvæ in the food-plant.

The pupe of P. napi are either green or have a bonecoloured ground with black markings and minute dots. The latter may be classified, according to the amount of

pigment, as:-

(1) Dark, (2) Intermediate, (3) Light. In the light forms the pigment is so small in amount that the pupæ are practically bone-coloured (3 a). The green pupse are equally deficient in pigment and may be regarded as a dimorphic form of this degree (3 b). These relationships may be conveniently expressed as follows:—

- 1. DARK.
- 2. Intermediate.
- 3. Light. (a) Bone-coloured. (b) Green.
- (1) The Dark pupe. The ground is bone-coloured. Black pigment is strongly developed on each side of the dorsal surface, forming a large sub-rectangular patch on each side of each abdominal segment, fusing into an irregular mass anteriorly, on each side of the thoracic region. The dorsal line is marked posteriorly by a distinct dot on each segment. Seven dots can be recognized, including one on the caudal spine. There is also a large pigment patch on each side of the mesothoracic keel and on each side of the anterior rostrum. Minute black points are scattered between the sub-dorsal pigment and that of the dorsal line.

On the sides, the principal development of pigment is on the wings, in which part of the venation is thus rendered conspicuous, while the outline of the hind margin of the future wing is marked by a distinct row of black dots. Near the centre of the wing is the "wing-mark" made up of two or more, generally three, intensely black patches—the largest inferior—apparently occupying spaces between the veins. Even in the darkest forms these patches are nearly always conspicuous from their superior blackness: they often tend to fuse, forming in many cases a single large patch.

The eye is strongly pigmented superiorly, but below and including the crescentic mark upon which alone of the entire pupal surface the facetted structure is developed

(the pupal eye), it is devoid of pigment.

(2) The Intermediate pupe. The ground is bone-coloured. These pupe differ from the last, with which they are connected by transitional forms, in the lesser development of black pigment both dorsally and on the wings. As a rule the diminution is proportional throughout, but in certain cases the dorsal pigment may retain its full development.

The lesser amount of black pigment renders the intense

black patches in the centre of the wing especially distinct

and sharp.

(3) The Light pupe. (a) Bone-coloured. These also are perfectly transitional into the Intermediate pupe. In pupe of this degree the pigment is everywhere reduced, remaining strongest in the black patches in the centre of the wing, which become excessively conspicuous against the pale bone-coloured ground. In some of the most extreme cases these patches become much fainter, but a trace of them is probably always to be found. In other parts the pigment spots and patches are much smaller, and are often represented by minute dots: on the eye

it is often absent altogether.

(3) The Light pupe. (b) Green. Pigment is never highly developed upon the ground-colour of these pupæ. With very rare exceptions it does not exceed the amount present on the light bone-coloured pupe (3 a). The green pupæ are far more transparent than the bone-coloured, and the palest are even more deficient in pigment than the palest of the bone-coloured forms. The most important difference in marking has already been mentioned, viz. the absence of the black patches in the centre of the wing (the "wing-mark") even when pigment is developed elsewhere as greatly as in a decidedly dark bone-coloured pupæ of the corresponding degree (3 a)—a pupa which would always possess distinct and prominent patches. Occasionally, however, faint traces of the marking may be detected, as minute dots, even in the palest green forms, and very rarely it is fully developed. All marked exceptions will be described below. In the centre of the wing the transparency is such that a considerable depth into the pupa can be seen, and the large tracheæ distinctly made out.

Before classifying Mr. Merrifield's numerous pupæ, I am tempted to suggest what I believe to be the meaning of this strange dimorphism in marking. The possible failure of my hypothesis would not, however, alter the validity of the observations which I have here recorded. Without attaching too great weight to it, I do not hesitate to suggest the hypothesis, thinking it possible that observa-

tion and thought may be stimulated by its means.

I have just alluded to the great transparency of the green pupe  $(3 \ b)$ , and have stated that this is especially marked in the centre of the wing, viz. in the exact position of the dark mark on the bone-coloured pupe  $(3 \ a)$ .

These latter are also, though less transparent than the

green, chiefly so in the same area.

The green pupæ resemble green leaves and stems, and Mr. Merrifield's experiments show that they are produced by such surroundings: the bone-coloured pupæ resemble, and are produced by, such surfaces as bark, wood, or stone.

Now the transparency is no hindrance to the concealment of the former: it is rather an advantage. But to the latter it is a distinct hindrance and, when once seen, immediately betrays the fact that the pupa is not the opaque object to which it presents so strong a superficial resemblance. I believe that this is the reason why this particular area is so invariably covered up by dark patches of pigment in the pale bone-coloured pupæ of this species. I believe that the persistence of this particular mark when the other pigment spots and masses are disappearing in the palest pupæ, is due to the operation of natural selection.

The experiments and observations Miss Cora B. Sanders and I were able to conduct, in the summer of last year, prove that pupæ (in this case of Vanessa urticæ) are subject to a tremendous struggle for life: they also strongly indicate that the enemies are guided by their sight in hunting for them. Hence it appears to me that there is nothing improbable about the suggestion that this dark patch covering the transparent area may have been retained by natural selection in certain forms, because transparency would be a danger, may have been dismissed in certain others, because transparency would be an advantage.

The pupæ were compared and tabulated on Dec. 22nd, 1898, and on the following dates in 1899—Jan. 6th, 7th, 9th, and 28th. Nearly all of them were extremely healthy, and showed the effects of the conditions in a remarkable manner. As these are the first complete and detailed experiments which have been conducted upon this sensitive species, and the material was in such excellent condition, the comparison was carried out with the utmost care, and numerous details were recorded which are included in the tabular statement below. The order is that in which the pupæ of *P. machaon* were considered so far as the conditions were the same. The conditions which were different are placed at the end.

It is to be observed that the light-green forms (3 b)

		Deg	grees o	f Pup	al Col	our.	
Experi	MENTS.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (6)	Totals	Remarks.
1. Black.		6	4			10	Three of the (2)s very dark.
2. Black (pupæ fixed to	compartment o black).	15	1	1		17	(2) Very dark: (3 a) very light. Also two dead pupe which were probably (1) or (1) and (2).
3. Miscella compartment.	neous black		1			1	
4. Black th (in shade).	nrough glass			1		1	Very pale pupa.
5. Black co	empartment,		2	1		3	The (3 a) darkish.
chier as 6 mos	nterior group stly close to rglass front.	5	6	6		17	Pupæ mostly fixed parallel to glass front: the heads of only five pointed towards light, and only two of these pointed directly (the body line at right angles to glass front).
a sheet of glass we and will be est est.  Society. (See	oup half-way ween back front, and ards inner (viz. near- orange).	1	1			2	One pupa pointing towards light; one had become loose.
ning roof. ning roof. The wh	roup in pos- or inner cor- of roof.	1	1			2	Another pupa had died and is not classified: another was accidentally mixed with next group and is there classified. All four towards light (direct).
sheet Sheet	oup in poste- outer corner extending ag outer side oof.	10	2			12	Including one pupa from last-named group. All pupæ towards light and all direct except one.
7. Black con or near from	ompartment nt glass	3	7	4		14	One (3a) rather dark with an indistinct wing-patch; another much lighter with a faint one. In addition, an extraordinary intermediate form not tabulated—a pale green ground with the pigment of a (2).

	-					
	Deg			l Colo	ur.	
Experiments.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (6)	Totals	Remarks.
8. Dark sticks.	2	4	1		7	Another pupa had died. The (3 a) was dark.
9. Dark sticks: pupæ fixed to bottle.		1		1	2	The (3 b) very pale and pigmentless.
10. Dirty white paint.	9	15	5	2	31	Two had died and are unclassified. It is certain that neither was green. One pupa was withdrawn as a P. rapæ. One (3 b) dark but no wing-mark to be detected.
11. Glass of old cage.		3	4		7	All light for their degrees except one (3 a).
12. Darkness.		1		6	7	Of the (3 b)s two are deep green with much pigment for this degree, two similar with little pigment, two pale and almost pigmentless.
13. Dead reeds.		4	4		8	Wing-mark faint in three $(3a)$ ; two of them dark for this degree.
14. Dead reeds; pupæ on glass.			1	1	2	(3 b) deep green with little pigment.
15. Dull green reeds.		3	7	1	11	(3 b) pigment very dark, equal to darkest (3) or even light (2): wing-mark small but dark. One (3 a) with very slight wingmark. The (2)s light.
16. Dull green reeds; pupæ on glass.			3		3	Another pupa dead. Wing-mark indistinct in one.
17. Oat-straw.			3	2	5	(3a) wing-mark indistinct in two. (3b) one pale, one deep green, both with very little pigment.
18. Oat-straw; pupæ or bottle.	1		2		2	Pupæ with little pigment and wing-marks indistinct

	Deg					
		te		t (3)		
Experiments.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (b)	Totals	Remarks.
19. Dutch "gold" on sticks.			8		8	Six pupæ with very little pigment. Wing-mark very faint in two, invisible in one.
20. Dutch "gold" through glass.				1	1	Deep green; little pigment.
21. Dutch "gold" on glass.			1		1	Almost pigmentless except for very distinct, dark wingmark.
22. Green paper spills.			7		7	Another pupa dead. Five pupæ with very little pigment, and wing-mark indistinct, or even invisible.
23. Green paper, through glass.			1		1	Very little pigment.
24. Green paper, on glass.				1	1	Very little pigment; deep green.
25. Green cabbage-leaves; pupæ chiefly on bottle.			4	6	10	Another pupa dead: $(3a)$ s very light, but with wingmark conspicuous. $(3b)$ s pale green except one, all with little pigment.
26. Green cabbage-leaves; pupa on white muslin.			1		1	Very pale pupa with faintly transparent yellowish appearance.
27. White paper.			6		6	Very little pigment; wing-mark distinct and dark on three, indistinct on one, hardly visible on two.
28. White paper, through glass.			1		1	Almost pigmentless.
29. Yellow paper.			1	7	8	Nearly all pupe almost pigmentless. The $(3 \ a)$ transparent yellowish and really transitional to $(3 \ b)$ . Of the latter, two pale, two intermediate, and three deep green.

		1 -		4.5			1
		De	grees o				
			te	-	ht (3)	1	
	Experiments.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (b)	Totals	Remarks.
	30. Yellow paper, through glass.			1	1	2	The (3 a) is transparent greenish-white, and transitional to (3 b). The latter deep green with much pigment for this degree.
	31. Yellow paper, on glass.			1		1	Like the (3 a) described above and, like it, very pale and pigmentless.
	32. Orange leno bag.				11	11	Two pale, nine deep green. One of former fixed to a leaf. Seven with very little pigment and the others not very dark.
-	33. Orange-yellow compartment; miscellaneous pupæ.				8	8	Another pupa dead. One pale, two intermediate, five deep green. All very pigmentless except three of latter (not very dark), and one remarkable deep green form with the pigment of a (2) and a small distinct wingmark; also present on two of the last-mentioned set of three.
	34. Orange compartment, tear leno and dirty white paint.			1	3	4	(3 a) very pale and pigmentless with no wingmark. (3 b) one pale, two deep green, all dark pigmented; faint trace of wing-mark on one.
Same soor. The bule on the	Anterior scattered group, many close to clear glass front.  The group wellow half of			1	13	14	Five pupæ parallel to glass front (four close to it), one with tail, seven with head; pointing directly to light: one with head to light, but body line not direct (viz. forming angle of about 45° with front). (3 a) very pale, transparent, and pigmentless, much more so than any on the black side of same sheet. One (3 b) pale

]		Deg	rees o	f Pupa	l Colo	ur.	
	Experiments.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (3)	Totals	Remarks.
other (black) half have yellow "through glass							yellowish-green, and really transitional to $(3 a)$ . It and five others almost pigmentless, six with very little pigment, and one with much, like a dark $(3 a)$ and yet hardly a trace of wing-mark. Twelve of the $(3 b)$ distinct green ground.
other (black) half have already been tabulated (6) on page 396. yellow "through glass."	Compact group in the outer side of the middle part of roof (viz. away from the black).			1	7	8	Heads of all pupæ directly point to light. The (3 a) very pale, but more pigmented than any green (3 b) in this group and with traces of wingmark. (3 b) all distinct green and very little pigment.
ted (6) on page 396.	Group in the inner side of the middle part of roof (towards the black).			1	8	9	Another pupa dead. All heads pointed directly to light. (3 a) with very little pigment. Seven (3 b) similar, and one darker, but no trace of wing-mark. All (3 b) distinct green.
All pupæ were on orange-	Elongated group along outer side of posterior part of roof.	f			13	13	All directly faced light except one parallel with front and two reversed (tails directly pointing to light). All distinct green, and, except three, with very little pigment.
orange-	Inner side of posterior part of roof.				1	1	Distinct green, very little pigment. Directly faced light.
36. glass	Orange, throug	h			3	3	Another pupa dead. One pale, two deep green; all very pigmentless.

	Deg	rees o	f Pupa	al Cole	our.	
			-	t (3)		
EXPERIMENTS.	Dark (1)	Intermediate (2)	Bone- coloured (a)	Green (b)	Totals	Remarks.
37. Orange compartment; leno through glass.			2	3	5	(3 a) very pale and pigmentless. (3 b) one pale, two deep green, one of latter with medium pigment, other two very pigmentless.
38. Orange-yellow compartment, on or near front glass.		1	19	6	26	Another pupa dead. (2) very pale. (3 a) ten pupa very pale and pigmentless with wing-mark minute, faint, or absent; of these two are greenish and transitional to (3 b). Six are light with wing-mark prominent. Three rather darker, but only average for this degree. (3 b) one pupa pale, five deep green. Two almost pigmentless (including pale one): four rather dark for this degree and minute wing-mark on two.
39. Planed deal, in light.		1	3		4	(2) very pale. Very little pigment on (3 a)s and very faint wing-mark on one: prominent on others.
40. Planed deal, in shade.			5		5	Four with very little pigment, but wing-mark distinct: one typical.
41. Planed deal, on glass lid.			1		1	Very pale and pigment- less, but wing-mark dis- tinet.

which presented any trace of a "wing-mark" are specially so described: when no reference is made to this character it may be assumed that it was absent in (3 b)s, normal in (3 a)s.

I will now briefly summarise the results obtained with this highly interesting and sensitive pupa. For the sake of brevity (3 a)s are called *light* pupæ; (3 b)s green pupæ. Black (1 to 7). The very powerful effect of black in

TRANS. ENT. SOC. LOND. 1899.—PART IV. (DEC.) 27

producing the darkest pupæ is very clearly seen. The black paper did not act quite as strongly through the thickness of glass (4, 5, 6) as when the pupæ were in direct contact with it. When the pupæ were upon the glass window at a varying distance from the black paper, the effects were much less marked (7). Black in shade (4) produced an *intermediate* pupa, but the parts of the roof of case (6) which were farthest removed from the light produced pupæ which were rather darker than those nearer to it.

Dark sticks (8) produced as great an effect as black, but

little or no influence was exerted at a distance (9).

Dirty white paint (10) gave rise to a great variety of pupæ, all forms being represented among the thirty-one forms tabulated, the dark and intermediate degrees (1) and

(2) strongly predominating.

Clear glass (11) produced intermediate and light pupe, while in Darkness (12) they were strongly green—six out of seven being (3 b). This result is so remarkable and extreme an effect of darkness that further experiments are to be desired. It is probably to be explained by the strong normal tendency of this species to produce green forms in the absence of any effective stimulus (see 9, 14, 24, in support of this: the pupe on the glass removed from the stimulus are greener than those subjected to it).

Dead reeds (13) produced intermediate and light pupæ;

at a distance (14) light and green ones were formed.

Dull green reeds (15) produced chiefly light pupe (3 a) with some intermediate (2) and a single green one (3 b); on the glass they were all light (16).

Out-straw (17) caused the puper to become light (3 a) and

green (3 b), while at a distance they were light (18).

Dutch "gold" (19, 20, 21) tended strongly towards light pupæ (3 a), the only exception being in the case of a green pupa (3 b) formed when the gilt surface was the other side of glass (20). At a distance (21) the single pupa was similar to those fixed on the gilt.

Green paper (22, 23, 24) produced almost exclusively light pupæ (3 a), the action through glass (23) being similar to that of the coloured surface itself. At a distance a

single green pupa (3 b) was formed.

Green cabbage-leaves (25, 26) on the other hand produced far more green than light pupe, affording a most interesting comparison with the artificial colour. On this point see the Appendix in which the constitution of the light reflected from the latter is described. The pupa on white muslin (26) was light (3 a), and probably affected by this

surface rather than the leaves.

White paper (27, 28) is of great interest, invariably producing light pupe (1 a); the influence through glass (28) being the same as that exerted directly (27). We see in this and in the pupe produced by Dutch "gold" (19—21) a great advance in the susceptibility of these pupæ over those of the Vanessidæ. Thus the highly sensitive pupa of V. io is influenced in the same direction by bright green (such as those of nature), yellow and orange as it is by golden metallic surfaces and by white. These all alike tend to produce brilliant green pupæ with a golden sheen over much of the surface. And yet such pupæ would only be concealed on the bright green backgrounds. The pupa of P. napi is similarly influenced by bright green, yellow, and orange, but is quite differently affected by white and gilt. The pupe in the latter case are light bone-coloured (3 a), and certainly much more effectually concealed on a white surface than if they were green. Traces of the same kind of sensitiveness at a much lower level of development are rendered probable in Papilio machaon from the results already recorded, and will be seen to exist in Pieris brassica and P. rapa, in the formation upon a white background of intermediate, grey, and pale forms rather than green ones. The similar effects of bright green, yellow, and orange are certainly to be explained as they have been in many other species, both larvæ and pupæ, by the fact that all these colours reflect a high proportion of the effective rays, viz. the yellow and orange. This will be proved in the case of P. napi by the results of the spectroscopic examination of the backgrounds which were made use of (see Appendix).

Yellow paper (29—31). Produced only the light (3 a) and green pupe (3 b), the latter strongly predominating. The influence through glass (30) and at a distance (31) was less strong in the direction of green, although the number of pupe was too small to carry much weight.

Orange leno and paper, in some cases combined with yellow (32—38), were even more powerful than the yellow in producing green pupæ (3 b); in fact if we consider those experiments only in which the pupæ were directly placed on the backgrounds or were only separated by the thickness of the glass (32, 33, 35, 36, 37), no less than sixty-

seven green pupæ (3 b) were formed as against five light ones (3 a). The influence through glass (35, 36, 37) was undiminished; but that at a distance (34, 38) was immensely reduced, a single intermediate pupæ (2), a large number of light (3 a), and only a few green (3 b) being produced.

Planed deal (39—41) seemed to produce effects comparable to those of white, viz. that form of pupa out of the various possible degrees, which harmonized best with the background, viz. light (3 a), a single intermediate one (2) also appearing. No appreciable difference is to be noted between the effects in strong light (39), shade (40) and at a distance (41).

Looking at these experiments as a whole, the much smaller effect produced by the coloured backgrounds upon the pupæ "on the glass," viz. at a more or less distance from the effective stimulus, harmonizes well with

the results of previous investigation.

The strong tendency of the pupe, or rather the larve, to face the light directly is well shown in the results of Experiments (6) and (35) where the positions are recorded. The great majority of the exceptions were due to the larva placing itself parallel and in close proximity to the clear glass front. A similar tendency to seek the angles between a horizontal and vertical surface probably in part explains the fact that so high a proportion directly faced the light, the body line having been drawn into parallelism and often into contact with the sides. In these experiments only one pupa was parallel with and close to the back, but I have noticed very many pupæ of Pieris brassicæ in shallower breeding-cases, in this position. The few complete exceptions in (6) and (35) in which the head pointed directly away from the light are enough to show that susceptibility is unaffected by orientation.

Mr. Merrifield is to be congratulated in having proved the high degree of sensitiveness possessed by this pupa. While the susceptibility is as great as that of any other species, even of the highly sensitive Vanessa io, the range of controllable modification is probably wider than in any other as yet investigated in sufficient numbers. This is shown by the production not only of green and dark forms, but of pale and grey pupæ upon such backgrounds as white paper and planed deal. At the same time the range is not nearly so great as that of the larva of Amphidasis betularia, which can produce on appropriate dark

surfaces many distinct shades ranging through black, brown, and grey; and also on the provision of the appropriate stimuli can become white or green (Trans. Ent. Soc. 1892, l. c.).

The reactions of the pupe of *Pieris napi* to the colours employed agree well with the observations recorded in the case of other susceptible pupe if allowance be made for the wider range of controllable modification.

## E.—EXPERIMENTS UPON THE PUPÆ OF Pieris brassicæ.

## 1. Experiments upon the Winter Pupæ of Pieris brassicæ. (F. M.)

I took advantage of the pestilential abundance of the larvæ of this species to experiment on them and I exhibit samples of the results, which will be described so far as necessary in the following section. It is the less necessary to refer to them at any length, because the species has been so fully experimented on by Prof. Poulton as described in the papers before referred to, and as will appear later in this memoir, also during the present year (1898). But I would call attention to one feature, that has been carried perhaps a little further than had been done before, in my experiments on this species and the next referred to, P. rapæ. It seemed a fair inference both from Prof. Poulton's paper and from my personal observation of the experiments with darkness on the other two species, that the positive application by reflection or otherwise of some decided colour (including black and white among colours) was necessary to affect the colour of the pupe in a marked degree. Accordingly I tried the experiment of surrounding some pupe with clear glass away from all near reflecting objects. For this purpose I placed the full-fed larvæ in clear glass cylinders covered by clear glass and resting on a clear glass sheet several inches above the table, so that light reached them all round. They were placed on a table It will be observed that in the case near the window. both of this species and the next, the pupe of the larvæ thus exposed to uncoloured light on all sides, rather closely resemble those in darkness, the former being somewhat darker than the later. In the case of P. napi darkness produced much variety of colour: of seven all but one are green but of somewhat varying tint, and the one bone-coloured and two of the green ones are much spotted with dark.

I found this species very troublesome as to the place of its pupation. In no one case did I succeed in getting it to pupate on a stick whatever its colour, and it had a way of pupating on the clear glass in front of the cylinder or bottle. To circumvent it I procured some white photographic trays, some of which I covered with orange glass, and others with deep green glass, while one was lined with black paper and covered with clear glass, and another, left white, was covered with clear glass. The space left between the bottom of the tray and the glass covering varied from about  $\frac{1}{4}$  inch to  $\frac{3}{8}$  inch or a trifle more, and in some cases it will be seen the pupa bears marks of squeezing. These instances are indicated by the word "screen," in the case of trays thus provided with screens of coloured glass, "tray" where the covering was clear glass.

The whole of the pupæ obtained (about 80) are displayed, part in the Exhibition Case, and part in the glass-topped

boxes.

### 2. RESULTS OF THE ABOVE EXPERIMENTS. (E. B. P.)

The pupe of *P. brassica* were compared May 3rd and May 6th, 1899, the results being shown in the following table (see pp. 407, 408). The degrees of pupal colour are the same as those suggested and fully described in Phil. Trans. 1887 (*l. c.* pp. 409, 410). The letters *g. o. w. y.* indicate the faint greyish *green*, *orange*, *yellow*, or *white* tint of the pupæ in the darker degrees. The tint is however usually very faint, being greatly obscured by the dark pigment (see also Trans. Ent. Soc. London, 1892, p. 439).

These results afford a very useful confirmation of those which have been previously obtained. Thus the black (1, 2, 3) produced uniformly dark pupe, the effect being as strong when the dark surface was behind glass (3) as when it formed the surface to which the pupa was attached (1, 2). The black surroundings also produced a considerable effect upon pupe which were attached to the

clear glass at some distance (4).

Darkness (5) produced far more intermediate pupæ, although still upon the dark side of intermediate. As Mr. Merrifield has suggested, this result is to be compared in an interesting manner with that of clear glass (28). It is probable that in these two cases we witness the results of pupal tendencies undirected by any effective stimulus.

1	_					
Experiments.	D	EGREES O	F PUPAL	Coloui	RS.	Remarks.
EXPERIMENTS.	Dark- est. (a)	Intermediate. $(\beta)$	Light. $(\gamma)$	Whitish Yellow. (2)	Green. (3)	Nemarks.
1. Black.	1 0	3 g				The darker pupa dead.
2. Black tray.	1 w	2 g,y				Also one dead and one emerged: both probably (1 $\beta$ ).
3. Black, through glass.	1 g	2 g				
4. Black, on glass.		4 w, y g, g				Also one dead, probably a $(1 \beta)$ .
5. Darkness.		2 g,o	3 g,w,y			Probably one more pupa accidentally transferred to those on clear glass.
6. Green paper.		1 <i>y</i>	1 <i>y</i>	2	1	
7. Green gauze.				1	. 1	
8. Green, through glass.			2 w,g	3	1	
9. Green screen.				1	1	Also one dead, probably (2); and one emerged; not darker than (1 γ).  The (3) was a peculiar greyish-green.
10. Green, on glass.			3 g,g,w	3	1	Also one dead; a $(1 \gamma)$ , or darker.
11. Cabbage leaves.			2 g	1	1	Also one dead, evidently a (2) or (3).
12. White.		1 w		1		
13. White paper (cylinder).		1 <i>y</i>				
14. White paper.		2 w,g	1 y			Also one dead, but certainly a $(1 \beta)$ .
15. White calico.		2 y,w	1 w			
16. White tray.		1 w			1	
17. White, on glass.			2 y	1		

	Di	EGREES OF	F PUPAL	Colour	RS.	
EXPERIMENTS.		Intermediate. $(\beta)$	Light.	Whitish Yellow. (2)	Green.	Remarks.
18. Yellow paper.					2	Also one dead.
19. Yellow, in shade.		3 0,9,9				Also one dead, but probably a (1 $\beta$ ).
20. Yellow, through glass.			2 w,y			
21. Yellow, on glass.				1		
22. Yellow compartment, on glass with patch of white paper behind.					1	
23. Orange leno.		1 w	1 g			Also one dead or emerging, about a $(1 \beta)$ .
24. Orange.			1 w	1	1	
25. Orange, through glass.					1	
26. Orange screen.				4		
27. Orange on glass.				1	3	One (3), a curious greyish form.
28. Clear glass.		6				Also one dead, probably a (2) or (3). The (1 \beta)s are, one greyish-orange, four green, one white.  Probably one pupa belongs to the group in darkness.

Green paper, gauze and cabbage-leaves (6, 7, 8, 10, 11) caused the appearance of far lighter pupe, the majority being the whitish-yellow degree (2). Here too the influence through glass (8) was as strong as in the other experiments (6, 7). The few pupe subjected to light through green glass (9) were of the two lightest and greenest degrees, thus confirming the effects described in Trans. Ent. Soc. Lond. 1892 (pp. 429-432, 446, 466—

468), and ascribed to the greater concentration of the effective rays. The stimulus produced a strong effect at a distance (10). The powerful effect of a natural green

environment (11) is of great interest.

The experiment with white (12—17) was especially useful, as this environment had been almost omitted from the previous investigation of this species. It is at once seen that the effect is to produce intermediate pupæ, inclining towards the dark side. In this, the results differ widely from those obtained with Vanessa urticæ and V. io in which white surroundings produced strong effects in the direction of the golden and green pupæ respectively. There is great uniformity in the results obtained by the different white backgrounds, and the action at some distance (17) was clear. It will be found that my own experiments (43 to 48) in 1898 (see pages 415, 416) lead to the same conclusions as those which result from Mr. Merrifield's.

Yellow surroundings (18 to 22) produced the usual strong effects in the direction of the palest, greenest pupæ, the influence being much reduced in shade (19), and also reduced when acting through glass (20). An influence at

some distance was probably exerted in (22).

Orange surroundings (23 to 27), for the most part, produced the same effect as the yellow, the orange leno (23) being an exception. Influence was strong through glass (25), and at some distance (27). The orange screen (26) produced considerable effects, in accordance with the principles already explained (Trans. Ent. Soc. Lond. 1892, l. c.); although an even stronger result might have been expected.

This account of the results should be read in relation to the Appendix, in which the colours reflected from the

various backgrounds are analyzed.

# 3. Experiments upon the Winter Pupæ of Pieris brassicæ. (E. B. P.)

I also took advantage of the immense abundance of this species to repeat some of the experiments made in previous years upon insufficient numbers. The larvæ in part came from St. Helens, Isle of Wight (experiments 5, 6, 37, 38, 39, 40), partly from St. Helens and near Reading (13, 41, 42), and partly from St. Helens and near Oxford (remaining experiments, including those with conflicting colours,

and excepting Nos. 4 and 12). They were collected by Miss Cora B. Sanders (St. Helens and Reading), by Mr. W. Holland (Oxford), Mr. A. H. Hamm (Oxford), and by myself (St. Helens). Experiments 13, 41, and 42 were conducted by Miss Sanders; 5, 6, 37, 38, 39, and 40 by me, and the remainder by Mr. Holland and Mr. Hamm. I wish to express my warm thanks for all the large amount of kind help I have received.

The conditions of experiment are sufficiently shown in the following tabular statement (see pp. 411—416), the constitution of the reflected light being given in the Appendix.

The pupe were examined on May 6, 7, 8, 9, 10 and 11, 1899, when several of them had emerged or were emerging. All these, however, are indicated below, and nearly

all could be tabulated with considerable accuracy.

The positions of the pupæ in relation to the receptacles employed and to the light were noted in a large number of examples, with the following results. Thirty-six pupæ were fixed to the roof (or in the angle between it and the back), with a direction parallel with the front (generally clear glass) and back; 25 were fixed to the front, back, or sides in a vertical position with the head uppermost (including a few with the head downwards—cases in which pupation certainly occurred during a temporary reversal of the position of the receptacle); 41 were fixed, almost invariably to the roof, with the head pointing directly towards the light, viz. with the line of the body at right angles to the front (generally clear glass); 11, otherwise similarly placed to the last, had their heads pointing directly away from the light; 15, otherwise similar, had their heads obliquely directed towards the light; 10 their heads obliquely directed away from it. It is therefore clear that there is, upon the whole, a tendency to direct the head towards the light, although the tendency is not nearly so strongly marked as in P. napi. There was no appreciable difference in the colour according as the head pointed towards or away from the light.

Reviewing the results of the tabulated experiments, the effect of black (1 to 9) is, with certain exceptions, similar to that which has been obtained before, and also to Mr. Merrifield's investigations carried on simultaneously. These exceptions are the very dark pupe obtained in almost complete darkness (8), and the very unusual light-

ness of some of those in dim light (6, 7).

			-		1			
				(1)		ish-	en.	
	Experime	ents.	Dark.	Intermediate. $(\beta)$	Light. $(\gamma)$	Whitish-	© Green.	Remarks.
(wide a	and low,	d cylinder placed on lass front).	1					On roof near and parallel with glass front. Emerging.
	2. Black lined cylinder (very similar to last).		3	1 <i>y</i>				Similar position to above; together with three other dead pupæ (unclassified). Two of the (1 a) greenish, the other emerged.
der (in betwee arrange	ntermedia n 7 and ement) rtments,	lack cylinate in size 24, same with two moderate			1 <i>y</i>			Pupa on black paper roof of upper compartment.
4. T ford.	arred fen	ce near Ox-						Two pupæ found April 2, 1899, by Λ. H. Hamm. They were very dark, probably (1 β) or even (1 α).
Box placed on one short Illumination moderate.	ned box 25.5 n section; 9.5 ow 11 c.m. by	Attached to roof.		4 g,g,w?	4 g, o, o, u			One $(1 \beta)$ emerging. Also seven dead, four probably $(1 \gamma)$ , two $(1 \beta)$ or $(1 \gamma)$ , and one uncertain. Also one emerged, and was a $(1 \gamma)$ . Pupæ chiefly in two crowds of seven to R., and five to L. of roof. The heads were nearly as often away from light as towards it; often oblique, and often parallel with back or front.
side.	c.m. c.m. 13.5	Loose on floor.			1 g			Also one dead; it had been a $(1 \gamma)$ .
6. Box very similar to last, but window a little smaller.	Attacl	hed to roof.		4 w, w, o, o	1 y	2	1	Also six dead; $1 = (1 \beta)$ , $4 = (1 \beta)$ or $(1 \gamma)$ , and $1 = (1 \gamma)$ . Also two emerging, a $(1 \gamma)$ and a $(1 \gamma)$ or $(2)$ . A group of four at back and of ten on left side, heads of those (six) not parallel with back nearly always turned to light.
r to last, but	Attack net wind	ned to black dow.		1 y				Also three dead on the sides of box; all $(1 \gamma)$ or rather lighter or darker than this. Also one dead, loose on floor—a $(1 \beta)$ or $(1 \gamma)$ .

		(1)		-i		
EXPERIMENTS.	Dark.	Intermediate. $(\beta)$	$(\gamma)$	Whitish.	© Green.	Remarks.
7. Small black compartmented cylinder, in deep shade. The cylinder about 10 c.m. high by 6 c.m. in diameter. A black paper partition divided the cylinder into two chambers illuminated by a narrow window 2 to 3 5 c.m. wide.					1	Pupa from a single larva put in lower compartment. Rather more pigment than usual, but deep green ground. Pupa fixed vertically, head upwards, at top of side opposite window, but latter closed above and the roof very convex below, so that larva had been in deep shade.
8. Black cylinder in almost complete darkness: 16 c.m. diameter by 10 c.m. deep.	10	3 g			•	All pupæ isolated. All $(1 \beta)$ very dark and two of them nearly $(1 \alpha)$ .
9. Black-lined (3 sides) rectangular glass case (18 c.m. square by 28 c.m. high) with perforated zinc roof.	1 0, g	3 0, 9 ?				Four pupæ isolated on roof; the $(1 \alpha) g$ , on clear glass window, just below black binding and zinc at top, and near black paper of side.
10. Perforated zinc roof of yellow-lined (three sides) rectangular glass case (28 c.m. square by 38.5 c.m. high).		4 o, o, g, g	1 0			Also one emerged; was a $(1 \beta)$ or $(1 \gamma)$ . All tabulated pupe on roof in groups of two and three.
11. Similar zinc roof of similar white-lined (3 sides) case (23 c.m. square, by 33 c.m. high).	1 w	2 0				Also one dead, probably a $(1 \ \gamma)$ or $(2)$ . All pupe isolated on roof.
12. Brown paper.		1				Found in O. U. Museum by A. Robinson. Probably an escape from my cases. Imago had emerged, but pupa so dark it may have been even a (1 \alpha).
13. Salmon-pink box in strong light (24 c.m. by 13.5 c.m. in section in front).					1	All sides and roof sloped inwards to a back only 10 c.m. by 18 c.m. This caused a very strong illumination.
14. Orange paper-lined cylinder (22 c.m. diameter, 10.2 c.m. deep). Placed on side with clear glass front.		-	1		2	Also one emerged, a (2) or (3). The $(1 \gamma)$ bright yellowish green. All pupe on roof,

		- 3					
			(1)		sh-	0.	
Exp	PERIMENTS.	Dark.	Intermediate. $(\beta)$	Light. $(\gamma)$	Whitish.	(S) Green.	Remarks.
der (27 c.1	nge-lined cylin- n. diam. 8 c.m. ranged as the			1 g		2	One (3) on glass front, three-quarters up. Others on roof.
der (30.5	nge-lined cylin- c.m. diam. 9.8 ). Arranged as					4	Also one emerged, evidently a (3). One of the (3)s had the pigment of a $(1   \gamma)$ but bright green ground of a (3). All pupe on roof.
Four-compartmented Each compartment 10 deep. Box placed on front.	17. Compartment I.					3	Two on roof, one on floor. The box had clearly been turned over for a time, so that floor became roof.
npartn partmer x place	18. Compartment II.				1	2	All on roof.
Four-compartmented orange-lined box. Each compartment 10 c.m. square, 6.4 c.m. deep. Box placed on side with clear glass front.	19. Compartment III.			1 g		2	Also one emerging—a (2) or (3). Two on roof, one on angle of roof and side, one head downwards on side; clearly due to box having been turned over.
ined box. e, 6.4 c.m. clear glass	20. Compartment IV.						One pupa emerging, but probably a $(1 \gamma)$ ; one dead, but was a $(2)$ or $(3)$ . Both on roof.
Compartments 4.5 c.m. by 3.75 c.m. in section, 5.3 c.m. deep.	21. Compartment H, orangelined.				1		On back, close under roof.
by 3.75 section, deep.	22. Compart- ment L, orange- lined.			-		1	In angle between roof and back.
23. Lower compartment of small orange-lined cylinder, similar to 7.						1	In angle between roof and side.
of large ora der (8 c m c.m. high,	er compartment nge-lined cylin- n. diam. by 18 with window wide) arranged o 7.			-		1	Position of pupa clear although emergence had occurred. On roof, close to side.

			(1)		4.		
Exi	PERIMENTS.	Dark.	Inter- mediate.	Light.	Whitish Yellow.	Green.	Remarks.
		(a)	(B)	(γ)	(2)	(3)	
gular glass square,	nge-lined rectan- s case (30.5 c.m. 41 c.m. deep) with clear glass		1 g	1 y	3	3	Also two dead, a (2) and a (2) or (3). One of the (2)s tabulated was loose on floor: all the rest of the pupe on roof. The darkest pupe in dim illumination.
Eight- partment section, side with	26. Compartment E, orange-lined.					2	On roof,
Eight-compartmented box. Compartments 12—13 c.m. by 14 c.m. in section, 8.4 c.m. deep. Placed on side with clear glass front.	27. Compartment F, orange-lined.			•		3	Two on roof, one on side. Also one dead on side and one on roof; both probably (3) or one perhaps (2).
m. by 14 eep. Pla front.	28. Compartment G, orange-lined.				2	1	All on roof; one emerged and one emerging, but position seemed certain.
Com- c.m. in aced on	29. Compartment H, orange- lined.			1 0	1		Also one emerged, almost certainly a (2). All on roof.
In same box as 21 and 22. A wider and E narrower box than H and L.	30. Compartment A, yellow-lined.					1	Pupa loose on floor.
In same boxas 21 and 22. A wider and E narrower oxthan H and L.	31. Compartment E, yellow-lined.						One pupa dead on roof, a (2) or (3).
	er compartment llow-lined cylin- lar to 24.				1		Pupa on side just below roof.
Eight-comp compartment viz. 26 to 29	33. Compartment A, yellowined.					1	In back corner of roof.
1 00 00	34. Compart. ment B, yellowined.				2		One on roof, one on back: latter with the green ground of a (3).
ented bou	35. Compartment C, yellowined.				1	1	Pupæ isolated on roof.
r. These her four,	36. Compartment D, yellowined.			4 o, g, g, y		1	Four crowded, one isolated $(1 \gamma) y$ on roof.

	90					
		(1)		ish-	n.	
EXPERIMENTS.	Dark.	Intermediate. $(\beta)$	Light. $(\gamma)$	Whitish-	© Green.	Remarks.
37. Yellow-lined box placed on side, 20 c.m. square, 6 c.m. deep. Window 14.5 c.m. square, yellow leno covered.		1 0	1		9	Also one dead, but clearly a (3). Four (3) and the $(1 \beta)$ on yellow leno window. Six (3)s on roof.
38. Yellow-lined box placed on long side: 14 c.m. by 18.5 c.m. in section, 8.5 c.m. deep. Window 10.5 c.m. by 15 c.m. as above.				9	3	Also two dead, probably a (2) and a (1 $\beta$ ) or (1 $\gamma$ ). All pupe on roof; mostly in small groups.
39. Yellow-lined box placed on short side: 21 c.m. by 12 c.m. in section, 9 c.m. deep. Window 8 c.m. by 15.5 c.m. as above.			1 g	4	3	Also five dead, two emerged and one emerging, but all certainly (2)s or (3)s. Ten on roof, six on left side (three (2)s and three dead).
40. White box (31.5 cm. by 16 c.m. by 6 c.m. deep) with yellow leno window (11 c.m. by 23.5 c.m.), probably placed upwards.			2 g, y	2		Also three emerging; they were either $(2)$ or $(3)$ , or in one case possibly a $(1 \gamma)$ . All attached to edge of leno, where pasted to box.
41. Green cabbage-leaves.				1	6	All seven on separate leaves, except that there was another dead one, certainly a (3), on the same leaf as one of them. Also one pupa dead, but certainly a (3), and two emerged, both (2) or (3). Also a pair on one leaf, one dead and one emerged, both certainly (3s).
42. Dark purple-lined box with white roof, in very dim light: (12 c.m. by 19.5 c.m. by 7 c.m. deep).			6 g	9	1	Also six dead probably three (2)s, one (2) or $(1 \gamma)$ , one (2) or (3), one $(1 \beta)$ or $(1 \gamma)$ . Also one emerged; probably a (2). All tabulated pupe on white roof, except two (2)s, loose on floor. All pupe very much undersized.
43. White opal gas globe (usual size).				1	1	Pupæ isolated in upper part of globe.

Experiments.		Dark.	(1) Intermediate.	Light.	Whitish-	Green.	Remarks.	
		(a)	(B)	(γ)	(2)	(3)		
Four- lined be clear gl same as	44. Compartment A.			2 g			Pupæ on roof, isolated.	
box, placed on s glass front. Di as 17 to 20.	45. Compartment B.		1 g			1	Also two dead or emerging, probably $(1 \beta)$ , or perhaps $(1 \gamma)$ in one case. All pupe on roof, three crowded.	
nented on side	On sid Ment C.	1 g	1 y			One on roof, one on floor (case having doubtless been turned over).		
ed white- side, with Dimensions	47. Compartment D.		2 g		1		Two on roof isolated, one on back.	
48. Rectangular glass case with three sides lined with white paper, and white opal glass roof (20.4 c.m. square, 30.6 c.m. high).			2 g	1 g			Two pupæ isolated on roof. One (1 \(\beta\)) on black binding of angle between window and side, but close to white paper.	

The effects of a dull surface of perforated zinc (9—11) and of brown paper (12) were, as might be expected,

practically the same as those of black.

Salmon paper (13) acted like orange (14—29), and produced the lightest and greenest form of pupa. The results of so many experiments with orange are very striking, especially as a very deep reddish-orange surface paper was employed.

Yellow (30-40) also produced striking results in the same direction, but not equal in the proportion of the

greenest pupæ, to those of orange.

Green cabbage-leaves (41) acted like orange.

Experiment 42 was very mixed, the pupe being, almost all of them, fixed to a white surface in a dark purple box in a very dim light. They were strongly on the light side of intermediate.

White (43—48) has been already described as producing pupæ on the dark side of intermediate (see p. 409). There are, however, some few marked exceptions in both Mr. Merrifield's and my experiments, in which the lightest and greenest pupæ were obtained.

Thus Mr. Merrifield's and my experiments in 1898

afford most useful confirmation in the case of a species which has not been hitherto sufficiently tested, besides bringing evidence of its behaviour under conditions as yet hardly tried at all. In the next section is recorded an experiment upon the same species, which, more than all others, needed repetition because of the important conclusions which follow from it.

## 4. Experiments with Conflicting Colours upon the Winter Pupæ of Pieris brassieæ. (E. B. P.)

I had long been anxious to repeat some of these experiments upon the species of *Pierinæ* because of their extreme suitability for such an investigation and because of the

important conclusions which follow from the results.

It had been originally supposed by Mrs. M. E. Barber (Trans. Ent. Soc. 1874, p. 519) that particoloured pupe are produced by a particoloured surface—a conclusion which naturally followed from the views held by many at that time as to a direct "sun-picture or photograph" on the fresh, moist skin of the pupa. A single pupa of *Papilio* 

nireus had seemed to support this conclusion.

In 1886 I made a large number of conflicting colour experiments on Vanessa urtice (Phil. Trans. 1887, l. c. pp. 368-392). The contrasted colours were, however, only applied during Stage III when the larvæ are suspended preparatory to pupation and are less sensitive than at an earlier period. Nevertheless the results were sufficient to make it highly improbable that any parti-coloration of the pupal surface could occur as the result of such a mixed stimulus, and led to the conclusion that the effects were due to the intermediation of the nervous system in the central parts of which the opposing influences from different regions of the body met and produced more or less of an equilibrium, resulting in the dispatch to all parts of the body surface of stimuli producing intermediate effects. These conclusions were so far-reaching and important that it was necessary if possible to repeat the experiments with other species in which the conditions were more favourable. Although such experiments were not made in 1886 upon the Pierinæ, it was clearly seen, when the paper came to be written, that they would be peculiarly suitable for the purpose, because of the great length of the whole sensitive period and the fact that its two stages are both passed under conditions which are eminently favourable for such

TRANS. ENT. SOC. LOND. 1899.—PART IV. (DEC.) 28

an investigation. A few such experiments upon *P. rapæ* were attempted by G. C. Griffiths in 1887 (Trans. Ent. Soc. 1888, pp. 265, 266), and the results upon the whole supported those obtained in the case of *V. urticæ*. But the experiments were not very convincing because the colours employed were not those which produce the most

marked and opposite effects.

In 1888 I made some experiments of the kind upon P. rapæ and P. brassicæ (Trans. Ent. Soc. 1892, pp. 445, 446 and 484), using a box lined with black and orange squares, but owing to the excessive mortality from the attacks of ichneumons only 6 of the latter and 2 of the former could be tabulated. The results however entirely confirmed the experiments made in 1886 upon V. urticæ, intermediate and not parti-coloured pupæ being always obtained. In 1892 I made a large number of experiments upon Vanessa io (l. c. pp. 420-426), and again upon V. urticæ (l. c. pp. 391—397). Furthermore a method had by then been arrived at which enabled the larvæ of the Vanessidæ to be subjected to conflicting colours during the whole of the sensitive period; and another method whereby the dorsal and ventral surfaces could be subjected to opposing stimuli (in the case of V. io, l. c.). In all previous experiments the anterior and posterior parts of the body had been thus treated. All such modifications and additions yielded confirmatory results.

I was nevertheless very anxious to repeat the experiments upon the *Pierinæ* and therefore took advantage of the abundance of *P. brassicæ* last year (1898). Here, again, however, owing to the *Ichneumonidæ*, my results were not at all what I had anticipated; but taking them in combination with those which have been already

published they leave little or no room for doubt.

Two conflicting colour-boxes were made for me by Mr. W. Holland and Mr. A. H. Hamm. The first box had an internal section of 54.5 c.m. by 14.2 c.m., and a depth of 7.4 c.m. (from back to front in the position made use of). It was used resting on one long side with a clear glass front. The roof (the side uppermost in the position in which a receptacle is used is here always called the "roof") was divided into 9 bays of about equal size by means of 8 hanging partitions (each 7.4 c.m. deep and thus extending from the back to the clear glass front, and hanging down for a distance of 3.5 c.m.); while the back

was similarly divided into 10 bays by 9 partitions which alternated with those of the roof. These were 9.0 c.m. high and their lower borders 2.0 c.m. from the floor, while they projected 3.5 c.m. from the back towards the glass The object of this division of the internal surface was to separate the larvæ as much as possible, and thus minimise their influence upon each other during the sensitive period. The whole internal surface, except the floor, of the box, and both surfaces of all the partitions were lined with a chess-board pattern of orange and black, each 1.4 c.m. square, and thus as nearly as possible half the length of an average mature larvæ of P. brassicæ when resting in Stage II preparatory to pupation. pattern was made by ruling the outlines of the squares in pencil upon a sheet of deep orange surface paper and then carefully pasting black tissue-paper squares over alternate orange squares.

It is much to be regretted that an experiment conducted with so much care should have produced such limited

results as regards the numbers of pupæ.

The first box only contained 3 pupe which could be tabulated with certainty on May 6th when the examination was made. All were fixed in the left-hand bay of the roof, near to the glass window.

One pupa was fixed diagonally across a black square with the end of its tail lying on another one, and the head, directed towards the light, overhanging an orange square.

It was dead but had clearly been a (2) or a (3).

The second was fixed parallel with the glass, the posterior  $\frac{3}{5}$  of its body on the anterior part of a black square, but a little overhanging an orange square in front, and the anterior  $\frac{2}{5}$  similarly on orange and overhanging black as well as orange in front (viz. towards light). It was a

greenish  $(1 \beta)$ .

The third pupa was also parallel with the glass, although the tail curved towards it. The posterior  $\frac{2}{3}$  of its body was on the posterior (viz. away from glass) border of (so that the right side overhung) a black square, the anterior  $\frac{1}{3}$  similarly on and similarly overhung orange. The left side (away from glass) overhung the opposite colours in each case except the posterior  $\frac{1}{6}$  which curved towards light, viz. towards the middle of the black square, so as to overhang black. The pupa was a greenish  $(1 \gamma)$ .

There were also two other dead pupæ which could be

placed with tolerable accuracy, by an examination of the

persistent cuticular pigment.

One of these pupe was at the back of the roof in the same bay as those described above. It was chiefly upon the black, extending obliquely across parts of two black squares which were in contact at the junction of its anterior and middle thirds; at this point therefore and on each side it, the sides of the body overhung orange. There was very little pigment and it had been certainly not darker than a  $(1 \gamma)$ , and probably either a (2) or (3).

The second pupa was on the roof of the bay at the opposite end of the box, close to the hanging partition. Its anterior half was on black, its posterior on orange, crossing almost at the middle of the adjacent sides of the squares; its head towards the light. It had probably

been a  $(1 \beta)$ .

Although these five pupæ had been subjected to the most strongly contrasted influences in various regions of their bodies, there was not, in a single instance, the faintest trace of parti-coloration. The opposing influences gave rise to a general effect which was almost exactly intermediate between the effects which they would have respectively produced if they had acted alone. It is to be noted that if there is any deviation from the intermediate position it is in the direction of the effects produced by orange. The larvæ seem upon the whole to have rested in contact with black in preference to orange, and thus overhung the latter colour rather more than the former. But many more experiments would be required in order to estimate exactly the relative strengths of these two opposing influences; and it is noteworthy that the results of my experiments upon this species in 1888 led to different conclusions upon this point.

The second box was 43.6 c.m.  $\times 15.4$  c.m. in internal section and had a depth of 10 c.m. It was similarly arranged with 6 hanging partitions, and 7 projecting from the back each 8.5 c.m. long but in other respects

similar.

The second box was examined on May 7th. In this case six had pupated on the glass. Of two isolated pupæ, fixed in a vertical position with head uppermost, one had emerged and one was dead or emerging; both were probably (1 y). Two more, similarly placed, were dead and could not be classified. Of two near together, but otherwise similarly fixed, one was a greenish  $(1 \gamma)$  and

one, emerging, was probably a  $(1 \gamma)$  or (2).

Two pupæ were fixed to the parti-coloured surface of the roof. Of these one diagonally crossed two black squares in a manner very similar to that of the first described of the two dead pupæ in the first box, which could not be classified with certainty. The direction of the body was oblique with the head away from the light. It had emerged, but had clearly been a (2) or (3). The second was fixed in another bay, near to and parallel with the glass. The posterior  $\frac{2}{3}$  of the body crossed a black square, the anterior  $\frac{1}{3}$  was on the next orange one. It had emerged but had evidently been a  $(1 \beta)$  with quite dark pigmentation. There was no trace of less pigmentation in the anterior third of its body.

These results entirely confirm those obtained in the

Although further experiments of this kind are to be desired, especially upon so sensitive a species as P. napi, it may be regarded as certain that the conclusions derived from the earlier experiments with conflicting colours are sound, and that not parti-coloured pupe but uniform intermediate ones are obtained in this way.

### F.—NOTES ON THE STRUGGLE FOR EXISTENCE IN THE LARVÆ OF Pieris brassicæ. (E. B. P.)

I have previously noted the numbers of this species which perish from the attacks of parasites in a year in which the larvæ are specially abundant. It seemed of interest to obtain further records, and I accordingly asked Mr. Holland and Mr. Hamm to keep notes of the number of larvæ attacked by ichneumons and the numbers dying apparently from other causes, which they removed from the cases containing the mixed larvæ from St. Helens and Oxford (see p. 409). The results are recorded in the table on the following page.

In the breeding-cases from which these larvæ were removed only 121 pupæ were taken, including the dead ones; so that the extinction is on a vast scale. Even if it be conceded that the larvæ dying without the appearance of parasites, and the dead pupæ, were entirely due to the conditions of experiment (such as the possible introduction and spread of some form of bacterial disease), the extinction due to the attacks of a single species of parasite is still immense, only about  $\frac{2}{7}$  of the whole surviving it.

			Number of Larvæ attacked by Ichneumonidæ.	appar	ber of deaths rently due to her causes.
1898.	Sept.	22	23		_
	,,	23	25		_
	,,	24	70		_
	,,	26	227		20
	,,	27	64		18
	,,	28	96		29
	,,	29	47		3
	,,	30	54		71
	Oct.	1	37		2
	,,	2	107		_
	,,	3	2		49
	,,	5	145		32
		6	42		7
		8	35		17
		11	11		5
1899			at least 31	at least	20
			Total 1016	Total	273
1899	"	6 8	42 35 11 at least 31		7 17 5 20

# G.—EXPERIMENTS UPON THE PUPÆ OF Pieris rapæ.

# 1. Experiments upon the Winter Pupæ of Pieris rapæ. (F. M.)

The next experiments tried were on this species and are detailed in the following section. I was late for this species and did not experiment with more than 50 or 60 larvæ, from which I obtained the single row of about 40 pupæ which are now shown in the Exhibition Case. Here I call attention to the contrast between those in the black surroundings on the one hand and those in the green paper, yellow, or orange surroundings on the other, the green in this species seeming more effective than it proved with the other species and the yellow less so.

### 2. RESULTS OF THE ABOVE EXPERIMENTS. (E. B. P.)

The colour variations of the pupe of *P. rapæ* have been already described and figured (Phil. Trans. 1887, *l. c.* pp. 410, 411, Plate 26, figs. 31—41), and it is here only necessary to state that the standard classification begins with the darkest pupe (1), ranging through the less dark (2) and still lighter (3) to the pale (4) and the green (5).

Mr. Merrifield's pupæ were compared on March 20, 1899: the results are given below without much detail,

inasmuch as the species is already known to be susceptible. In addition to those tabulated below, Mr. A. H. Hamm found two very dark pupæ, evidently (1), on a tarred fence near Oxford, on April 2, 1899.

All the (5)s were bright green and very pronounced

		Deg	grees o	f Pup	al Col	our.	
	EXPERIMENTS.	(I) Darkest.	Less dark.	Still lighter.	Pale.	Green.	Remarks.
		(1)	(2)	(3)	(4)	(5)	1
1.	Black.	2					Also 2 dead.
2.	Black, on glass.			2			Pinkish ground-colour.
3.	Dirty white paint.			1			Very dull, dark pupa. Removed from P. napi.
4.	Darkness.			4	1		(3) Pinkish: (4) greenish.
5.	Green.				1	1	Also 1 dead: (4) greenish.
6.	Green, through glass.				1		Also 1 dead or emerging. (4) light pinkish.
7.	Green screen.				1		Also 1 dead. Pupa greenish.
8.	White, on glass.				2		1 greenish, 1 pinkish.
9.	Yellow.				1	1	(4) greenish.
10.	Yellow in shade.				1	1	(4) greenish.
11.	Yellow on glass.					2	
12.	Orange.		1		1	2	Also 1 dead: (4) pinkish.
13.	Orange screen.					1	Also 1 dead (removed from P. napi).
14.	Clear glass.	1	3	1			Also 1 dead.

representations of this degree. A few other conditions were tried, but the single pupæ subjected to them had died and the colour had changed so greatly that they could not be tabulated.

The numbers of the pupæ are not large and the results quite confirmatory of previous experiments. (Phil. Trans.

1887, l. c., and Trans. Ent. Soc. Lond. 1892, l. e.: see also G. C. Griffith's experiments on this species in Trans.

Ent. Soc. Lond. 1888, p. 247.)

It is interesting to observe the relation between the effects of darkness (4) and those of clear glass (14). The latter produced even darker pupe relatively to the former than in the case of *P. brassicæ*.

The table does not support Mr. Merrifield's conclusion that the yellow (9, 10, 11) was less effective than in the case of *P. brassicæ*. The six pupæ were of the two lightest degrees, four of them green and the other two greenish.

The effect of the green and orange screens (7, 13) is confirmatory of previous results with other species (P, 13)

brassicæ and V. io).

It is not necessary to comment further upon the other results, all of which will be clear upon an inspection of the table on p. 423.

## H.—EXPERIMENTS UPON THE PUPÆ OF Vanessidæ.

# 1. Experiments upon the Pupæ of Vanessa urticæ and Pyrameis cardui. (C. B. S. and E. B. P.)

In the course of our investigations in 1898 into the struggle for existence during the pupal period of Vanessa urticæ it was necessary to produce a very large number of pupæ with colours as widely contrasted as possible. order to achieve this we made use of black surroundings on the one hand and gilt (Dutch "gold"), yellow, orange, and white on the other. There was abundant evidence in the 700 pupe which we obtained of the previously recorded influence of these surroundings, and also, to our frequent annoyance, of the effect of the dark surfaces of the larvæ upon one another. In fact so powerful was this influence and so gregarious were the larvæ under the conditions of our experiments that intermediate pupe were generally produced when the lightest forms were desired. The conditions of the investigation rendered it impossible to isolate so many larvæ in separate cases.

Many of the larvæ pupated on the leaves and stems of the food-plant (nettle), and when isolated brilliant golden

pupæ were almost invariably produced.

A few larvæ of *P. cardui* were also found and subjected to black and white surroundings: the pupæ being dark in the one case, and light, and often brilliantly metallic, in the other.

2. Experiments upon the Pupæ of Vanessa io. (Mabel E. Notley, Florence A. Wright, and E. B. P.)

The experiments of last year upon the struggle for existence during the pupal period are now being repeated in the case of *Vanessa io*. In this case all the pupæ were obtained at the outset of the investigation, and the results as regards their colour susceptibility can now be given.

We are greatly indebted to Mr. W. Farren of Cambridge, and to Mr. H. W. Head of Scarborough, who sent us numerous companies of larvæ in excellent condition. Kind help was also received from Mr. W. H. Harwood of Colchester, and from Mr. A. E. Holdway of Newton Abbot.

The larvæ thus obtained were placed in a large number of "light" and "dark" receptacles, the former being lined with orange, yellow, or white paper (white opal glass was used in the case of a few larvæ), the latter with black paper (a few were attached to the dull surface of perforated zinc). All were placed in a strong light and only shielded from the direct rays of the sun. A few were subjected to conflicting colours in one of the boxes described on pp. 418, 419.

The results obtained are tabulated below (see p. 426), the degrees of pupal colour being those described in Trans. Ent. Soc. Lond. 1892, p. 398; the (1)s and (2)s being the darkest forms with the underlying green completely or very nearly concealed by pigment which is blacker in (1), lighter in (2); the (4)s and (5)s being distinct green forms very bright and glittering in (5), duller and with more dark pigment in (4); the (3)s intermediate.

The pupæ which were attached to the nettle-leaves, leaf-stalks or stems are indicated by the letter n, and those found loose on the floor by the letter f. These facts were not however recorded at the beginning of the experiments so that more pupæ were in reality found in these positions in the companies received at first. The facts are important inasmuch as the pupæ on the floor were adversely influenced in the experiments with light surroundings, the pupæ on the nettles in the experiments with dark.

The companies are tabulated separately below, but it was not thought necessary to describe each separate receptacle, as this work is confirmatory. The numerous receptacles in which the larvæ of each company were placed are grouped together as "light surroundings," and "dark surroundings."

	1					-	,
Companies of Larvæ.	Conditions of Experiments.	(1)	Degree (2)	es of Pupal (3)	Colour. (4)	(5)	Totals.
Company of 64 larvæ (3 died), re- ceived July 11,				2	11	22 (3 n.)	35 (3 n.)
from W. Farren of Cambridge.	Dark surroundings.	4	9 (1 n.)	11 (3 n.)	1	1 (1 f.)	26 (4 n.) (1 f.)
Company of 172 larvæ (26 died), received July 11, from W. Farren of	Light surroundings.	1	2 (1 f.)	7 (3 f.)	26 (8 n.) (3 f.)	90 (21 n.) (3 f.)	126 (29 n.) (10 f.)
Cambridge.	Dark surroundings.	9 (1 n.) (2 f.)	(1 n.)	3 (1 n.)	1 (1 n.)	3 (1 n.)	20 (5 n.) (2 f.)
Company of 163 larvæ (16 died), received July 13, from W. Farren of	surroundings.		4 (1 f.)	2	2	72 (33 n.)	80 (33 n.) (1 f.)
Cambridge.	Dark surroundings.	10	44	9	1	3	67
Company of 87 larvæ (16 died), received July 14,	Light surroundings.	2	4	3 (1 n.)	3	31 (13 n.)	43 (14 n.)
from W. H. Har- wood of Colches- ter.	Dark surroundings.	8 (2 n.)	10 (5 n.)	4 (4 n.)	2 (2 n.)	4 (4 n.)	28 (17 n.)
Company of 57 larvæ (16 died), received July 14, from W. H. Har-	Light surroundings.		1	2	4 (1 f.)	29 (9 n.) (1 f.)	36 (9 n.) (2 f.)
wood of Colchester.	Dark surroundings.	3	1	1			5
Company of 148 larvæ (8 died), re- ceived July 14, from H. W. Head	Light surroundings.	4	1	13 (2 n.)	9 (1 n.)	83 (16 n.) (2 f.)	110 (19 n.) (2 f.)
of Scarborough.	Dark surroundings.	2	20	4 (1 f.)	1	$ \begin{array}{c} 3 \\ (2 \ n.) \\ (1 \ f.) \end{array} $	30 (2 n.) (2 f.)
Company of 18 larvæ (11 died), received July 15, fromTorquayfrom A. E. Holdway.	Light surroundings.					7 (3 n.)	7 (3 n.)
Company of 112 larvæ (21 died), received July 15,	Light surroundings.			4	3 (1 n.)	29 (11 n.)	36 (12 n.)
from W. Farren of Cambridge.	Dark surroundings.	15 (1 f.)	28	5 (1 f.)	5	(2 n.)	55 (2 n.) (2 f.)

			-		7		
Companies of Larvæ.	Conditions of Experiments.	(1)	Degree (2)	s of Pupal (3)	Colour. (4)	(5)	Totals.
W. Head of Scarborough.			13	11	15 (1 n.)	84 (10 n.) (2 f.)	123 (11 n.) (2 f.)
	Dark surroundings.	10	50 (2 n.) (1 f.)		1 (1 n.)	1	62 (3 n). (1 f.)
Company of 46 larvæ (2 died), received July 19, from H. W. Head of Scarborough.	Dark surroundings.	11 (1 n.)	19 (3 n.)	9 (2 n.)	3 (2 n.)	2	44 (8 n.)
Company of 139 larvæ (37 died) received July 19, from H. W. Head	Light surroundings.	1	7 (7 f.)	8 (2 n.) (3 f.)	5 (2 n.)	17 (1 n.) (1 f.)	38 (5 n.) (11 f.)
of Scarborough.	Dark surroundings.	8 (1 n.) (1 f.)	32 (5 n.) (14 f.)	19 (1 n.) (13 f.)	4 (4 f.)	1 (1 n.)	64 (8 n.) (32 f.)
Company of 25 larvæ, received July 21, from H. W. Head of Scar-	Light surroundings.			1	1	15 (4 n.) (1 f.)	17 (4 n.) (1 f.)
borough.	Conflicting surroundings.		1	2	5		8
Company of 70 larvæ (8 died), received July 21, from H. W. Head of Scarborough.	Dark surroundings.	20	31 (4 n.)	6 (4 n.)	3 (1 n.)	2 (2 n.)	62 (11 n.)
	Totals.	(1)	Degree:	s of Pupal (3)	Colour. (4)	(5)	Totals.
Companies experimented on in 1899, 13.	Light surroundings.	8	32 (9 f.)	53 (5 n.) (6 f.)	79 (13 n.) (4 f.)	479 (124 n.) (10 f.)	651 (142 n.) (29 f.)
Total number of larvæ, 1302 (180 died).	Dark surroundings.	100 (5 n.) (4 f.)	248 (21 n.) (15 f.)	71 (15 n.) (15 f.)	22 (7 n.) (4 f.)	22 (12 n.) (2 f.)	463 (60 n.) (40 f.)
	Conflicting surroundings.		1	2	5		8

These results prove the extreme sensitiveness of V. io, and they afford valuable and very extensive confirmation of some of the results described in Trans. Ent. Soc. Lond. 1892, pp. 397—432.

I.—EXPERIMENTS AND OBSERVATIONS UPON THE SUSCEPTIBILITY OF CERTAIN LEPI-DOPTEROUS LARVÆ AND PUPÆ TO THE COLOURS OF THEIR SURROUNDINGS. (A. H. HAMM and E. B. P.)

1. Stauropus fagi. Mr. W. Holland and Mr. A. H. Hamm of the Hope Department, who are extremely skilled and accurate observers, drew my attention last year (1898) to the fact that the larvæ of this species differ in tint according as they are reared upon beech or birch, and that the colours are in each case such as to conceal them.

During the present year Mr. Hamm reared two batches (from different parents) upon the same food-plant, beech, but in other respects under very different conditions as regards environment. One of the batches was reared in a white tissue-paper lined rectangular glass case with a perforated zinc lid, the other in a similar case lined with black tissue-paper. We compared the two, placing both

batches on white paper, on July 13, 1899.

There were 24 larvæ in the batch reared in the white case, and of these all but 2 were in the last stage and mostly advanced in it. All but 1 were much lighter than larvæ of this species usually met with in nature, and some most markedly lighter. The other batch consisted of 14 larvæ, of which 10 were in the last stage (mostly advanced), 1 in the last but one, and 3 in the last but two. All were very dark, and most of them far darker than those generally met with in nature. It is clear that this species is highly sensitive, and it would be of great interest to repeat the experiments under conditions which have been found in other larvæ to produce the strongest effects. It is remarkable that such considerable results followed from surroundings which were not apparently in contact with the larvæ (for these at any rate when they were examined rested upon the twigs and not upon the walls of the case). I do not think, in any of the previous experiments with larvæ, that equal effects have been produced in this manner; and one is tempted to enquire whether it is possible that the larvæ in earlier and specially sensitive stages, did actually rest upon the black and white walls of the cases.

2. Notedonta ziczac. My friend Mr. Arthur Sidgwick showed me, in the summer of last year (1898), a larva of

I was greatly struck by the remarkable lightness of its tint. It was quite unlike any larva of the species I had ever seen. Mr. A. H. Hamm informs me that he has also observed great differences in the depth of colour of this larva according to the food-plant upon which it has been found. It is highly probable therefore that this species is also sensitive, and searching experiments upon it are greatly needed.

This case and the last are of high interest, inasmuch as no larva at all closely allied to these two species has yet been shown to be sensitive to the colours of its environ-

ment.

3. Amphidasis betularia. Mr. A. H. Hamm tells me that he has again and again observed in nature the wide differences between the colours of this highly sensitive larva upon various food-plants, and that the differences are invariably in the direction of concealment. Mr. Hamm's experience in the field is so wide and his powers of observation so keen that the strongest confirmation is afforded to the observations recorded in my previous paper (Trans. Ent. Soc. Lond. 1892, pp. 359, 360).

4. Eupithecia pimpinellata. Mr. Merrifield informs me that Mr. Nicholson (of Lewes) has noticed that this larva appears in two forms—reddish-brown and green—which correspond to the two forms of the seed-heads of Pimpinella saxifraga on which it feeds. Mr. Nicholson states that the green larvæ are nearly always found on the green heads

and the others on the brown.

The power of colour adjustment is probably present in a very high degree in the larvæ of the genus, and numerous carefully conducted experiments are much to be desired.

5. Vanessa polychloros. I may also mention that a pupa of this species which I found (July 1899) upon the dark painted iron railing at the North Entrance Gate of the Oxford University Museum, harmonised very perfectly with the surface from which it was suspended.

6. Vanessa antiopa. In August 1897 I found several living pupæ of this species attached to fences, buildings, etc., at the Hunt Club, Scarborough Heights, Toronto. I specially noticed that there was a marked resemblance to the environment. This was all the more noticeable inasmuch as the colours differed very widely, some surfaces being very dark and others very light.

### K.—OBSERVATIONS ON THE COLOUR-RELA-TION BETWEEN A COLEOPTEROUS SPECIES (Cleonus sulcirostris) AND ITS SURROUNDINGS. (W. HOLLAND and E. B. P.)

The Rhynchophorous species Cleonus sulcirostris is described as possessing very variable markings (Fowler, British Coleoptera, London, 1891). Mr. W. Holland has recently found it upon the red sands of Boar's Hill near Oxford, and it is most interesting to observe that all the specimens are reddish-brown in colour, entirely different from the grey forms found by him on the sand-hills at Deal, and from the darker grey ones which he finds on Shotover Hill also near to Oxford and only a few miles from Boar's Hill. There are yellow and red sands on the top of Shotover, but Mr. Holland has as yet only searched for this species in localities where they are not exposed on the surface. There have been no exceptions to the colours of the very large numbers found on both hills. It is reasonable to suppose that these colours, which certainly harmonise with the ground of each locality, are protective; inasmuch as the species possesses in a very high degree the instincts which lead to concealment.

So far as I am aware this is the first time that such local adaptation of colour has been shown to occur in a Coleopterous insect, and the interesting question arises as to whether the species possesses the power of varying its colour during growth according to the stimulus provided by the colours of its surroundings, or whether the results are due to the varying operation of natural selection in different localities leading in each case to the survival of the individuals which are best concealed.

It will be of the highest interest to look for further examples in Coleoptera, as well as to attempt to ascertain the manner in which the colour adaptation is brought about.

### L.—APPENDIX.

THE QUALITY OF LIGHT FROM THE COL-OURED AND OTHER BACKGROUNDS EMPLOYED IN THE EXPERIMENTS RE-CORDED IN THE PRESENT MEMOIR. (SIR JOHN CONROY and E. B. P.)

My kind friend Sir John Conroy, F.R.S., again helped me to make a correct analysis of the light reflected from the backgrounds employed in our experiments. The papers, etc., were examined in the Laboratory of Balliol College, Oxford, on July 24th, 1899. The beam from an electric arc was passed through a bisulphide of carbon prism, and the spectrum thrown on a white paper screen in a darkened room. The coloured papers, etc., were held so as partly to cover the spectrum, and sometimes two were held in the spectrum side by side for purposes of comparison. The method was thus the same as that made use of on the previous occasion (Trans. Ent. Soc. 1892, l. c. pp. 459 et seqq.), except that the lime-light illumination was then employed, and our spectrum was therefore weaker at the blue end than with the electric The results obtained are recorded below.

I. Coloured backgrounds, etc., employed by F. Merrifield:—
Black net and black tissue-paper (used as a plane surface
and also rolled round sticks). The reflected light from
both gave a feeble continuous spectrum. The transmitted light was the same but still feebler.

Dark sticks also gave a faint continuous spectrum: cork carpet was similar except that the reflected red was prominent.

Orange tissue-paper (used as a plane surface and also rolled round sticks). Some absorption of green and more of blue and violet; absorption more marked in the sticks where there was more than one thickness of the paper. No appreciable difference between the reflected and transmitted spectrum of the paper. The spectrum was far more like that of a yellow paper than of the deep orange used in my experiments, which removed everything except the red, orange, and yellow.

Orange leno gave a very similar spectrum, the blue and violet being almost cut off, and the green a little darkened.

The absorption was more marked in the transmitted

light.

Yellow tissue-paper (also rolled round sticks). Violet cut off and blue much diminished; hardly any blue in the transmitted light, and in the thicknesses of paper rolled round sticks.

Golden yellow oat-straw gave a very similar spectrum, the blue and violet being absorbed and the rest unaffected.

Unfaded bright yellowish-green tissue-paper (also rolled round sticks). The red shortened and dimmed; the blue and violet much absorbed. Transmitted light similar, as also the reflected light from the paper round sticks.

Bright yellowish-green art muslin. A similar spectrum. Not much difference between transmitted and reflected light, except that two thicknesses produced far greater

effects in the former.

Dull green reeds. Whole spectrum somewhat weakened, the blue most and then the red.

Yellow metallic surface of brass (Dutch gold), also rolled round sticks. Appears to give a strong continuous spectrum, but the yellow colour is due to absorption of the blue end.

Dead reeds. The lightest of them gave a typical yellow spectrum with absorption of the blue end only; in the others there was diminution of all other regions, although the blue end was still most reduced.

Turned cylindrical wooden sticks (probably deal). A very similar spectrum; the blue end was still more absorbed than any other part, although less so than in the dead reeds.

Dirty white paint gave a very similar spectrum with some absorption throughout, most in the blue, least in the green.

White paper rolled round sticks, white calico, shaved white sticks all gave a strong continuous spectrum with no selective absorption.

Yellow glass (used as screen). Blue and violet cut off,

the rest unabsorbed.

Deep green glass (used as screen). The green almost unabsorbed. The whole of the blue end, and nearly all the red and orange absorbed.

II. Coloured backgrounds employed by E. B. Poulton and

those who worked with him.

The Black papers, both "surface papers" and tissue-papers, gave the same results as Mr. Merrifield's, and those previously recorded (E. B. Poulton in Trans. Ent. Soc. Lond. 1892, pp. 461—464), and the same was true of the yellow papers (surface and tissue) and yellow leno, all of which were typical; the white paper, and the white opal glass. The deep orange paper was similar to that I have previously used, and very different to Mr. Merrifield's. The following backgrounds had not been examined before:—

A dull surface of metallic zinc (perforated) gave a dim continuous spectrum (general, but no selective absorption).

Salmon pink surface paper. A very faint absorption of the blue was all that could be seen. The blue also looked redder, an effect which may have been due to the stray white light reddened by selective absorption in the paper.

Violet paper. Much of the blue end, and considerable red were reflected. There was an absorption band between the green and the blue, and the yellow, orange,

and green were much absorbed.



Merrifield, Frederic and Poulton, Edward Bagnall. 1899. "XIII. The Colour-relation between the pupæ of Papilio machaon, Pieris napi and many other species, and the surroundings of the larvæ preparing to pupate, etc." *Transactions of the Entomological Society of London* 47, 369–433. https://doi.org/10.1111/j.1365-2311.1899.tb00987.x.

View This Item Online: <a href="https://www.biodiversitylibrary.org/item/51000">https://www.biodiversitylibrary.org/item/51000</a>

**DOI:** https://doi.org/10.1111/j.1365-2311.1899.tb00987.x

**Permalink:** <a href="https://www.biodiversitylibrary.org/partpdf/21652">https://www.biodiversitylibrary.org/partpdf/21652</a>

#### **Holding Institution**

Smithsonian Libraries and Archives

#### Sponsored by

Smithsonian

#### **Copyright & Reuse**

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.