collection of Butterflies in the Solomon and New Hebrides groups, the details of which it was hoped would be laid before the Society at a future meeting.

The following papers were read :—

1. The Experimental Proof of the Protective Value of Colour and Markings in Insects in reference to their Vertebrate Enemies. By E. B. Poulton, M.A., F.Z.S., F.L.S., of Jesus and Keble Colleges, Oxford, Lecturer on Zoology and Comparative Anatomy, St. Mary's Hospital, Paddington.

[Received February 23, 1887.]

Introductory.—In the preparation of a short course of lectures which were delivered at the Royal Institution in the spring of 1886, I had occasion to work up the historical aspects of my subject :—"The Nature and Protective Use of Colour in Caterpillars." The results of this inquiry were thus expressed in the introductory part of the first lecture :—"When Darwin was investigating the bright colours of animals, and was elaborating his theory of their explanation as of use in courtship, he came across the brilliant colours of certain caterpillars and saw at once that they were a difficulty in the way of the theory. For caterpillars are undeveloped organisms ; they have been described as 'embryos leading an independent life," and there is no way of distinguishing the sexes by external colour or structure (except in a very few instances). Therefore we here meet with brilliant colours, often rendering the possessors conspicuous, which cannot be of any use in courtship. Seeing therefore that the bright colours must be of use in some other way, Darwin drew the attention of Wallace to the subject, and asked whether he could suggest any explanation. Wallace accordingly thought over the subject, and considered it as part of the wider question of the varied uses (other than sexual) of brilliant and startling colour, in other stages of insect-life and in numerous instances scattered over the whole animal kingdom, and he finally ventured to predict that birds and other enemies would be found to refuse such conspicuous caterpillars if offered to them. He believed, in fact, that such larvæ are protected by possessing a nauseous taste or smell, and that it is to their advantage to become as conspicuous as possible, so that their enemies are warned against a repeated experience of the disagreeable results which follow from tasting them, that in fact the gaudy colouring acts as an indication of something unpleasant about its possessor. It was then pointed out that, as far as experiment had gone, it had entirely confirmed Wallace's prediction. Conversely Wallace argued that larvæ which were inconspicuous, being coloured

so as to resemble their surroundings, would be eaten when detected, and this prediction also seemed to receive complete confirmation."

Thinking over the whole line of argument and its apparently complete confirmation, I was led to anticipate that a somewhat different method of conducting the experiments would lead to a modification and extension of Wallace's classification of the uses of colour, in the direction of greater elasticity. At the same time it seemed better to withhold the suggestion until I had taken the opportunity of submitting it to the experimental test. I was travelling in Italy a few weeks after delivering the lectures, and took the opportunity of capturing many individuals of a few species of South-European Lizards, and of one species of Tree-Frog (*Hyla arborea*, var. *meridionalis*). I was thus able to carry out the suggested experiments, which on the whole yielded results which confirmed the conclusions I had arrived at *à priori*, and also produced other results which I had not anticipated. Some of these results were shortly communicated to the Biological Section of the British Association at Birmingham (1886), and an abstract is printed in the volume containing the papers read at that meeting. The suggested extension of Wallace's line of argument, which has now been put to the proof, is as follows:— The acquisition of an unpleasant taste or smell, together with a conspicuous appearance, is so simple a mode of protection, and yet *ex hypothesi* so absolutely complete, that it seems remarkable that more species have not availed themselves of this means of defence. What can be the principle which works in antagonism to such a mode of protection? For in Wallace's theory no suggestion of a true counterbalancing limit appeared—*i. e.* one which increased with the increasing application of this method of defence, until the latter received a check or, for the time being, was rendered of no avail, or was even turned into an absolute danger. And yet it seemed probable that such an antagonistic principle would appear as the natural outcome of the too complete success of a method of defence which depends on the acquisition of an unpleasant taste or smell together with a conspicuous appearance. If a very common insect, constituting the chief food of one or more Vertebrates, gained protection in this way, the latter animals might be forced to devour the disagreeable objects in order to avoid starvation. And the same result might be readily brought about if a scarce and hard-pressed form adopted the same line, and so became dominant, after ousting many species which were much eaten by Vertebrates. If once the Vertebrate enemies were driven to eat any such insect in spite of the unpleasant taste, they would almost certainly soon acquire a relish for what was previously disagreeable, and the insect would be in great danger of extermination, having in the meantime become conspicuous by gaining warning colours. If the reasoning be correct, it is clear that this mode of defence is not necessarily perfect, and that it depends for its apparently complete success upon the existence of relatively abundant palatable forms: in other words, its employment must be strictly limited. It has, indeed, always been recognized that an insect may be distasteful to one Vertebrate

enemy, but palatable to another; and to this extent Wallace does point out a limit to the application of this principle of defence. But the counterbalancing limit which I suggested is of course entirely different, for I argued that a Vertebrate enemy may be forced by stress of hunger to eat an insect *although unpalatable to it.* Although the latter limit is thus quite distinct, it would certainly in time become identical with the former, as the distaste for the insect gradually disappeared after it had been repeatedly eaten. In fact it will be shown to be probable that many (if not all) of the instances in which an evidently distasteful insect is eaten by certain Vertebrates originally rose in this way. These suggested additions to Wallace's theory of protection by warning colours were capable of being put to the practical test. To achieve this object it was only necessary to ascertain whether an insect-eating Vertebrate could be induced by hunger to eat a gaily coloured and conspicuous larva which it was always known to refuse when other food was present, and which was evidently very much disliked on the few occasions of preliminary "tasting," which would always occur long before the time when the disgusting morsel would be reluctantly swallowed. I shall presently show that my suggestion was in every way confirmed by the test; but before giving an account of my own experience I will allude to all the previous experiments which have been made in support of Wallace's theory.

I. *Brightly Coloured or Conspicuous Larvæ.*

At a meeting of the Entomological Society of London (see Proc. Ent. Soc. ser. 3, v. p. lxxx, 1867) Wallace made his important suggestion as to the biological value of conspicuous and gaudy colours in caterpillars. It is obvious that the question of the value of such colours in the larval stage is almost the same as in other stages, and it was chiefly from the determination of the use in the latter case (due originally and principally to Bates) that Wallace suggested that a similar solution would be found to apply to the former also. Nevertheless there are reasons why such a method of defence is especially applicable to the larval stage. I have shown that there is a special reason in the anatomical construction of larvæ which explains why these organisms require to be defended from slight injuries (see Trans. Ent. Soc. Lond. 1885, pt. ii. Aug. pp. 321–323). A larva "may be described as a soft-walled cylindrical tube which owes its firmness, and indeed the maintenance of its shape, to the fact that it contains fluid under pressure. The pressure is exerted by the muscular parietes of the body. The advantage of this construction is as obvious as its danger; the larva possesses a motive force which can be applied to any movable part of the surface through the medium of the fluid." . . . "This construction is extremely dangerous; for a slight wound entails great loss of blood, while a moderate injury must prove fatal. The larvæ of *Smerinthus ocellatus* (and many others) nibble off each other's horns, and the wounded larvæ (although they do not seem to be aware of the injury)

ose a great deal of blood, and although they may recover, are generally stunted; and often I am sure the loss of blood proves fatal. If the wound be at all extensive, the fat-body and viscera protrude, owing to pressure on the side distal to the wound (that on the proximal side having been relieved by escape of blood)." Therefore it is that throughout the varied means of defence possessed by larvæ "the object is always the same—to leave the larva untouched, a touch being practically fatal." Wallace also originally expressed this peculiar danger incurred by larvæ in more general terms, viz. "their soft and juicy bodies are so delicate that if seized and afterwards rejected by a bird they would almost certainly be killed" (see 'Contributions to the Theory of Natural Selection,' 1875, p. 118). Other peculiar dangers of the larval stage will be pointed out below. Although it will be seen that brilliantly coloured and distasteful larvæ are often tasted by their Vertebrate foes when impelled by hunger, all observers agree that a second trial is rendered less likely because of the unusual appearance which accompanies the unusual and unpleasant effect upon senses other than that of sight.

Furthermore, I am now able to bring forward instances of very distasteful species which have no warning colours, but, on the other hand, are well disguised by protective tints and markings; and a comparison between the behaviour of Lizards towards these and the conspicuous species respectively, affords strong confirmation of the truth of Wallace's suggestion. It now remains to summarize the whole of the evidence in favour of the prediction made in 1867; for, after all, the question is purely one of evidence, and however convincingly the *à priori* arguments may be put, they are chiefly valuable as guides to practical investigation. And this is fully recognized by Wallace, who strongly urged the practical test upon the meeting at which his suggestions were first made. Experiments have been made by Mr. J. Jenner Weir, Mr. A. G. Butler, Prof. Weismann, and by myself. Jenner Weir (see Trans. Ent. Soc. Lond. 1869, part i., April) made use of the following birds in his investigations:—*Erithaca rubecula* (Robin), *Emberiza citrinella* (Yellow-hammer), *Emberiza schœniclus* (Reed-Bunting), *Pyrrhula vulgaris* (Bullfinch), *Fringilla cœlebs* (Chaffinch), *Loxia curvirostra* (Cross-bill), *Turdus musicus* (Thrush), *Anthus arboreus* (Tree-Pipit). He also used to a less extent *Carduelis spinus* (Siskin) and *Linaria minor* (Redpoll).

He obtained the following results:—

"All hairy caterpillars (experimented upon) were uniformly uneaten;" viz. *Arctia caja*, *Eriogaster lanestris*, *Porthesia auriflua*, and *Orgyia antiqua*. "None of these species were even examined." The writer believes that the hairs are not themselves disliked, but that they "serve as a caution to the birds that the larvæ so clothed are uneatable." This suggestion is supported by the fact that the young and comparatively hairless larvæ of *Spilosoma menthastri* were tasted by the Siskin, Redpoll, and by a West-African Finch (*Textor erythrorhynchus*), but these three birds evidently found the larvæ disagreeable, and soon left them alone. On the other hand the

more mature larva with its characteristic warning hairs was never even molested. It is probable that this explanation may be true of this and some other species, but it obviously does not apply in the case of *P. auriflua*, &c., in which the hairs themselves are a source of intense irritation and annoyance. Mr. Jenner Weir found the same results with the spiny larvæ of *Vanessa urticæ* and *V. io*, and he draws the same conclusions as to the meaning of the spines.

In this case the author states that "the metallic-looking chrysalides were also invariably rejected, thus showing that the spines were not the cause of the uneatableness of the larvæ." Experiments were also made with the following comparatively smooth-skinned, highly conspicuous caterpillars:—*Abraxas grossulariata*, *Diloba cæruleocephala*, *Anthrocera filipendulæ*, and *Cucullia verbasci*. In no case were these species molested. Thus these experiments strongly confirm Wallace's prediction. It may be doubted whether the larvæ of *Arctia caja* and of *Spilosoma menthastri* can be included among the brightly-coloured larvæ intended by Wallace, but there is no doubt that the habits of these species are such as to render them conspicuous in spite of their sober coloration. In Trans. Ent. Soc. Lond. 1870 (part iii., August), Jenner Weir has contributed another paper on the same subject. Mr. H. D'Orville, in the 'Entomologist's Monthly Magazine' (vol. vi. p. 16), had affirmed that the larvæ of *Cucullia verbasci* are eaten by birds in the wild state. In his second paper Jenner Weir conclusively showed that this species was not eaten in the wild state in certain localities, and he again proved that it was not touched in his aviary. It seems therefore certain that Jenner Weir is correct as far as his species of birds are concerned; but at the same time D'Orville seems to prove that this distasteful species may be eaten by certain birds. In this paper Jenner Weir confirms his previous experience with regard to *E. lanestris*, *D. cæruleocephala*, *A. grossulariata*, and *P. auriflua*. He also includes the following new species in the list of gaudy or conspicuous larvæ which were untouched by the above-mentioned birds:—*Odonestis potatoria*, *Lasiocampa quercus*, *Clisiocampa neustria*, *Hybernia defoliaria*. Of these the two first are hairy, and although with sober colour, are generally conspicuously placed on their food-plants. (I think it is also exceedingly probable that their rejection may be partially due to the possession of irritating hairs.) The two last-named larvæ are certainly brightly coloured.

Mr. A. G. Butler (Trans. Ent. Soc. Lond., March 1869, p. 27) only records experiments with three species of conspicuous larvæ. *Lacerta viridis* always refused the larva of *A. grossulariata*, but devoured that of *Phragmatobia fuliginosa*. The latter is not brightly coloured but, like the larva of *S. menthastri*, it is hairy and not inconspicuous. Frogs also refused the conspicuous larvæ of *A. grossulariata* and *Halia wavaria*, although this was often after tasting them, the rejection being accompanied by evident signs of disgust. The former larva was also rejected by Spiders, either with or without preliminary seizure. It is noteworthy that the larvæ would certainly be uninjured after being seized and then relinquished

by the Frogs, and probably in the case of the Spiders also (in fact, Mr. Butler states that this was the case), but a bite from a Lizard would always be very serious and generally fatal. Mr. Butler states that the Lizards seized the distasteful larvæ before rejecting them, although this may not have been in many instances. Mr. Butler has kindly given me an account of some further experiments upon birds, the results of which are included in the Tables below.

Professor Weismann ('Studies in the Theory of Descent,' Part II., pp. 336–340, English translation by Prof. Meldola) also experimented with *Lacerta viridis*, with the results that the following brightly coloured distasteful larvæ were refused:—*Clisiocampa neustria*, *Euchelia jacobææ*, *Pygæra bucephala*, *Pieris brassicæ*, *Deilephila galii*. On the other hand, the very highly conspicuous larvæ of *Deilephila euphorbiæ* were eaten, as also were those of *E. lanestris* and *Lasiocampa pini*. The young larvæ of *Lasiocampa rubi*, at a stage when they much resembled those of the rejected *E. jacobææ*, were eaten after cautious examination. Professor Weismann also regarded the larva of *Papilio machaon* (always rejected) as conspicuous; but from my own experience I should certainly consider it well concealed upon its food-plant, and I should exclude it from the category of conspicuous larvæ which support Wallace's suggestion.

My own experiments were conducted with green Tree-Frogs (*Hyla arborea*, var. *meridionalis*), and with Lizards of the following species:—*Lacerta viridis*, *L. muralis* (chiefly var. *tiliguerta*), and *Tarentola mauritanica*.

My diary, printed in the form of Appendix II. to this paper, will give all the details, dates, &c. of the various experiments made during the summer of 1886, so that it is unnecessary to further allude to them here.

Finally, when a few weeks ago I told Mr. Jenner Weir of my intention to bring together all the experimental evidence upon this subject, he most kindly sent me the notes of his own observations during 1886, for incorporation in this paper. His experiments were conducted with the following species of Lizards:—*Lacerta viridis*, *L. agilis*, and *Zootoca vivipara*, and the diary is also printed in full as Appendix I.

It now remains to tabulate the results of all the experimental evidence upon conspicuous larvæ detailed above or described in the Appendices. Before doing so, it is necessary to recall Wallace's original suggestion, "that brilliant or conspicuous larvæ would be found to be refused by their enemies:" that is to say, they will be found to possess some unpleasant attribute. This may be a disagreeable taste or a nauseous smell in the fluids and tissues of the larva, and perceived after it has been bitten; or it may be a strongly smelling fluid, discharged by certain special glands on the approach of an enemy (e. g. *Porthesia auriflua* with dorsal glands, or the Hymenopterous *Crœsus septentrionalis* with ventral glands; in both these cases the smell given off from the everted glands can be readily perceived as sharp or unpleasant to ourselves). The larvæ of *Pieris brassicæ*, or of *Pygæra bucephala*, &c., form instances of the former

class, although one cannot be sure that there is not some smell, given off from the general surface of the body. It will be shown that in some cases it is even likely that larvæ may be protected by their reputation for being indigestible. Again, the larvæ may be disliked because of the possession of irritating hairs, as in the case of *Porthesia auriflua*, in which the effects of the hairs are almost immediate and intensely irritating (to man, and evidently to lizards &c.); or as in other hairy larvæ which cause irritation after longer contact (e. g. *Odonestis potatoria*, from my own experience after long handling, and, as I hear from others, with *Lasiocampa rubi* and *L. quercus* &c.); but there is no doubt that the effects upon the delicate skin of the mouth would be much more rapid in all cases. We also see that more than one unpleasant attribute may be present in a single larva, as in the case of *P. auriflua*, &c.

Just as there may be many ways in which a larva may be unpleasant to its foes, there are many ways by which it may be rendered conspicuous, some of which have been suggested since Wallace's original hypothesis. Thus a larva may be conspicuous from its startling coloration (e. g. *P. auriflua* or *A. grossulariata*), or because it freely exposes itself, while its colours, although sober, do not harmonize with its food-plant (e. g. *O. potatoria* on grass, or *B. rubi* on heather). Again, it may become conspicuous by living in companies, in which case the individuals may be brightly coloured (e. g. *C. neustria*, *E. jacobææ*, *P. bucephala*, &c.); or may be sober-coloured, but strongly contrasted with the food-plant (*e. g.* the dark larvæ of *Vanessa io* or *V. urticæ*, freely exposed in companies on the tops of nettles). It is obviously of less importance for the gregarious species to be as conspicuously coloured as the isolated larvæ, because the numbers add greatly to the efficiency of comparatively sober colours. This explanation of the use of the gregarious habit in many species was made by Fritz Müller in 'Kosmos,' Dec. 1877, and an abstract of the paper was communicated to the Entomological Society of London by Professor Meldola (see Proc. 1878, pp. vi & vii). The descriptions of appearance in all the tables are principally taken from Newman's works, the habits being chiefly described from my own experience. Prof. Westwood has most kindly assisted me in the search for the names of many of the species employed in the experiments. (See Table I., pp. 198–203.)

A second small group of larvæ must be tabulated separately, *i. e.* those which take advantage of two methods of protection which at first sight appear to be mutually exclusive—the method of protective resemblance and that of a conspicuous appearance, warning of unpleasant attributes. Such larvæ are apt to pass unnoticed because of the harmony between their colours and markings and the artistic effect of their surroundings; but if discovered, or even if an enemy approach so that there is danger of their being discovered, the protective attitude is instantly changed for one which renders the larva conspicuous and warns the enemy of the presence of unpleasant attributes (taste or smell), or alarms it by the resemblance of the new appearance to some object of terror. These facts may even be

TABLE I.—*Undoubtedly*

Species of Larva.	Method by which rendered conspicuous.	Unpleasant attribute.	Results of	
			J. Jenner Weir, using many species of Birds and Lizards.	A. G. Butler, using Birds, *Lacerta viridis*, Frogs, and Spiders.
Pieris brassicæ.	Chief colours yellow and bluish green with black spots; also gregarious and freely exposed on upper sides of cabbage-leaves &c.	Taste or smell. "Disagreeable odour when crushed" (*Weismann*).	.....	.....
Vanessa io.	Intensely black, with minute white points; bristles; also gregarious and freely exposed on upper sides of nettle-leaves &c.	Ejects a green fluid from mouth when touched. ? Taste or smell. Proof lies in what follows.	Disregarded by all the birds.	.....
Vanessa urticæ.	Same as *V. io* in all respects except colour, which is lighter, although much darker than leaves of nettle; yellow often present on dark ground-colour.	Ejects a green fluid from mouth when touched. ? Taste or smell. Proof lies in what follows.	Disregarded by all the birds.	.....
Anthrocera filipendulæ.	Yellow and black; conspicuous position on trefoil &c.; so abundant locally as to be almost gregarious.	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds.	.....
Deilephila euphorbiæ.	Black, red, and yellow or white; most conspicuously coloured and freely exposed on the spurge.	"If interrupted they spit out a quantity of green liquid of an acid and disagreeable smell, similar to spurge-milk, only worse" (*Melhuish, in Stainton's 'Manual'*).	.....	.....
Deilephila galii.	Very variable colours, but always strongly contrasted, and "almost as conspicuous as *D. euphorbiæ*; rests fully exposed by day on the stem" [of *Galium*] (*Weismann*).	? Taste or smell. Proof lies in what follows.	.....	.....

Conspicuous Larvæ.

Experiments.		How far support given to Wallace's suggestion, that brilliant and conspicuous larvæ would be refused by some at least of their enemies.	How far support given to Poulton's suggestion, that a limit to the success of this method of defence would result from the hunger which the success itself tends to produce.
A. Weismann, using *Lacerta viridis.*	E. B. Poulton, using three species of Lizards and *Hyla.*		
Refused by *L. viridis.*	.....	Strong support.	No evidence, for other food was not withheld.
.....	.....	Strong support.	No evidence, for other food was not withheld.
.....	Eaten freely by *Lacerta muralis.* Not offered to others.	Support from behaviour of birds; shows that a larva may be disliked by one insect-eating Vertebrate and not by another.	No evidence, as above, from birds; of course the suggestion cannot apply to *Lacerta muralis,* which eat the larva freely.
.....	.....	Strong support.	No evidence.
Eaten at once by *L. viridis.*	.....	A difficulty, especially as also "sea-gulls and terns devour them in numbers" (*Newman*).	The correlation of a startling appearance with some unpleasant attribute must probably have existed once if not now. Have we a case in which hunger or opportunity have caused the enemies to neglect the latter, and therefore to benefit by the former?
Neither examined nor touched by *L. viridis.*	.....	Strong support.	No evidence.

TABLE I.

Species of Larva.	Method by which rendered conspicuous.	Unpleasant attribute.	Results of	
			J. Jenner Weir, using many species of Birds and Lizards.	A. G. Butler, using Birds, *Lacerta viridis*, Frogs, and Spiders.
Diloba cæruleocephala.	Yellow, green, and black; freely exposed on leaves of hawthorn &c.	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds. Experiment repeated a second season, when the larva was "examined when moving, but not eaten."	.....
Pygæra bucephala.	Yellow, orange, and black; downy; gregarious; most conspicuous on oak, elm, lime, birch, &c.	? Taste or smell. Proof lies in what follows.	Eaten by *Lacerta agilis*, but evidently disliked and generally avoided.	.....
Orgyia antiqua.	Black and pink, with hairy tufts; freely exposed on upper sides of leaves of nearly all garden plants.	Eversible dorsal glands doubtless yielding odoriferous secretion. Hairs also apparently disliked, and perhaps irritating.	Disregarded by all the birds.	A young Missel-Thrush reared from the nest has frequently eaten the larvæ, but the long hairs were always rubbed off before swallowing.
Porthesia auriflua.	Black, red, and white; hairy; very conspicuous on upper sides of leaves of hawthorn &c.	Eversible dorsal glands: secretion volatile and irritant. Hairs intensely irritating.	Disregarded by all the birds. Experiment repeated a second season. Refused by all the Lizards.	Eaten, without hesitation, by a young Sky-Lark, which, however, died soon afterwards with symptoms which may have been due to irritation from the hairs.
Euchelia jacobææ.	Alternate rings of black and yellow; gregarious; very conspicuous on ragwort.	? Taste or smell. Proof lies in what follows.	.....	.....
Lasiocampa (Dendrolimus) pini.	"Variegated with red, brown, grey, and white, with two blue fasciæ near the head, spotted at the sides with red; it is tufted with hairs, one thicker than the rest near the tail." Apparently conspicuous on its food-plant—pine. (*Westwood and Humphreys, 'British Moths.'*)	Curtis states that Walker found the hairs intensely irritating on handling the larva.	.....	.....

(*continued*).

Experiments.		How far support given to Wallace's suggestion, that brilliant and conspicuous larvæ would be refused by some at least of their enemies.	How far support given to Poulton's suggestion, that a limit to the success of this method of defence would result from the hunger which the success itself tends to produce.
A. Weismann, using *Lacerta viridis*.	E. B. Poulton, using three species of Lizards and *Hyla*.		
.....	.....	Strong support.	No evidence.
Avoided by *L. viridis*.	Eaten by very hungry *L. muralis*, and, I believe, by *L. viridis*, and yet evidently disliked by all.	Strong support.	Strong support.
.....	.....	Strong support in Jenner Weir's observation; and Butler's shows that the hairs are much disliked.	No evidence, for the Missel-Thrush appeared to relish the larvæ.
.....	*L. muralis*, when hungry, bit the larva, retaining it for a long time, but in the end rejected it, and much irritated by hairs.	Strong support, on the whole. It is impossible to decide whether the Sky-Lark was killed by the larvæ. If so, it strongly opposes the theory of any instinctive knowledge.	It is certainly a support to the suggestion that a Lizard when hungry enough should make such a determined attempt to eat the larva, which it evidently disliked.
Entirely disregarded by *L. viridis* until after another similar but palatable larva had been introduced; *then* tasted, but rejected.	Seized and relinquished by hungry *L. muralis*, Probably eaten later; but insufficient evidence.	Strong support.	It is certainly a support to the suggestion that a Lizard when hungry enough should make such a determined attempt to eat the larva.
Devoured by *L. viridis*, "but not exactly relished."	.....	Support.	Strong support. Eaten, although unpleasant in some way.

TABLE I.

Species of Larva.	Method by which rendered conspicuous.	Unpleasant attribute.	Results of	
			Jenner Weir, using many species of Birds and Lizards.	A. G. Butler, using Birds, *Lacerta viridis*, Frogs, and Spiders.
Eriogaster lanestris.	Black, red, and white; gregarious; living on a web; rather hairy; very conspicuous on hawthorn.	? Taste or smell. Proof lies in what follows. The hairs may be irritating.	Disregarded by all the birds. Experiment repeated a second season.	.....
Clisiocampa neustria.	Orange-red, black, white, and blue; rather hairy; gregarious, and living on a web when young; very conspicuous on apple &c.	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds, although very hungry. Eaten by *L. viridis* and *L. agilis*, although sometimes refused, and evidently disliked.	.....
Cucullia verbasci.	Green, yellow, and black; gregarious and very conspicuous on upper sides of leaves and on the stem of mullein.	The larvæ eject a green fluid from their mouths when disturbed. ? Taste or smell. Proof lies in what follows.	Disregarded by all the birds. Experiment repeated a second season.	.....
Halia wavaria.	Green to lead-colour, with yellow and black. Does not assume the characteristic highly protective attitude so common in Geometræ; but most conspicuous on currant and gooseberry.	? Taste or smell. Proof lies in what follows.	.....	Always refused by Frogs after tasting them; so also with Spiders. Supplied to the young of the Great Tit by the parent birds, and always eaten greedily.
Abraxas grossulariata.	Cream colour, black, and orange; as above, unlike most Geometræ, but *most* conspicuous on blackthorn, gooseberry, &c.	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds. Experiment repeated a second season. Once eaten by *L. agilis*; often tasted and refused; evidently much disliked.	Always refused by Frogs and *L. viridis* after tasting them; so also with Spiders. (*Epeira diadema* and *Lycosa*?, sp., were the Spiders used in the case of this and the previous species.)
Hybernia defoliaria.	Brown and yellow; as above, unlike most Geometræ, but conspicuous and often hanging by a thread from its food-plant (oak &c.).	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds.	.....

(*continued*).

Experiments.		How far support given to Wallace's suggestion, that brilliant and conspicuous larvæ would be refused by some at least of their enemies.	How far support given to Poulton's suggestion, that a limit to the success of this method of defence would result from the hunger which the success itself tends to produce.
A. Weismann, using *Lacerta viridis*.	E. B. Poulton, using three species of Lizards and *Hyla*.		
Eaten by *L. viridis*, "but not exactly relished."	.....	Strong support.	Support from Weismann's observation, which seems to show that the Lizard ate the larva, though not liking it.
Untouched by *L. viridis*.	Evidence insufficient, as the single larva which had disappeared may have escaped.	Strong support.	Strong support from Jenner Weir's observations with Lizards.
.....	.....	Strong support from Jenner Weir's observations. D'Orville states that they are eaten by birds in the wild state; Jenner Weir did not find this; and there must have been a difference in habit, perhaps due to the species of birds under observation or to extreme hunger.	No evidence from Jenner Weir. D'Orville's observations may possibly be a case in point.
.....	.....	Strong support, from the behaviour of the Frogs and Spiders.	The larvæ being tasted seems to point towards their being eaten in a condition of excessive hunger. The birds seemed to relish them.
.....	Generally unnoticed; but tasted by Frogs, and then rejected. Once chewed for some time by a hungry *L. muralis*, and then rejected.	Strong support. The most complete evidence afforded by any larva, and the most complete unanimity in observations, in which others agree as well as those quoted.	That hungry Lizards should often make determined attempts to eat so nauseous a larva is strong evidence for the suggestion; and it is seen that one Lizard succeeded in swallowing the larva.
.....	.....	Strong support.	No evidence.

true of gregarious larvæ. Thus a group of phytophagous Hymenopterous larvæ may remain inconspicuous while undisturbed, but nevertheless the approach of an enemy determines united movements in the colony which render the whole strikingly conspicuous, and which may be attended later by the emission of an offensive smell from the numerous ventral glands of all the individuals simultaneously (*e. g. Crœsus septentrionalis*). In the other larvæ which suddenly assume a terrifying attitude "the effects produced approximate somewhat to an intensely exaggerated caricature of a sort of generalized vertebrate appearance, probably of the serpent type (at any rate in *Chærocampa*), such as would be most efficacious in the case of birds. It is likely that the terrifying appearance of our own larvæ in temperate latitudes first arose in the tropics, where the imitated cause of alarm to the enemies of the larva is real and obvious. And it is probable that the success of the same method in countries where the reptilian fauna cannot be said to constitute a source of alarm is due to inherited memories of a tropical life which live on, as that instinctive fear of anything snake-like which is so commonly exhibited by the higher land-vertebrates including ourselves." (Poulton, Trans. Ent. Soc. Lond. 1886, pt. ii. June, pp. 156, 157).

The success of this combination of defensive measures depends on the extraordinary sensitiveness of the larvæ, so that the transition from the one method to the other is instantaneous, and in the case of the suddenly assumed terrifying attitudes, the enemy is additionally alarmed by the way in which some dreaded object seems, as it were, to spring into existence. It is very unfortunate that so few experiments have been made upon this most interesting group of larvæ.

Just as it was suggested that insect-eating Vertebrates might, under the influence of hunger, be induced to eat and finally to relish distasteful larvæ, so we must expect that the same cause would in the end prevent this elaborate system of intimidation from being successful. In this case, however, there is no prejudice against an unpleasant taste or smell to be overcome, and it is most probable that the larvæ would be in great danger as soon as the imposition was detected. It is perhaps on this account that these methods are adopted by an exceedingly small proportion of larvæ, but also because a certain size is necessary for any chance of success. Nevertheless this size is less than might be anticipated, for the anterior part of the body with large eye-like marks is generally swollen out into a resemblance to the head of a serpent, while the larval body is partially concealed among the leaves of the food-plant, and, in many positions, what is seen merely serves to suggest a far more extended length than that which actually exists. Wallace has suggested that it is very probable that the "spectacles" of the Cobra are terrifying marks, which warn the enemy against approach, and it is most interesting to note that the *Chærocampa*-larvæ mimic the terrifying eye-like marks of a Cobra-like serpent, and not the real eyes of a serpent, which are relatively small. (Table II., pp. 206, 207).

Having thus tabulated the results of experiments upon undoubtedly

conspicuous larvæ, in every way typical of the strongly coloured group to which Darwin had called the attention of Wallace, and having further tabulated those which become conspicuous on the approach of danger, it is now necessary to add a few other species which cannot be regarded as typical of the above-mentioned class, but which are not concealed or are very imperfectly concealed by protective colouring, which are more or less freely exposed upon their food-plants, or about which a difference of opinion exists. (Table III., pp. 208, 209.)

We will now consider a few of the conclusions arrived at by a study of the above tables, which give the whole of the experimental evidence (as far as I am aware) upon the precise question originally raised by Darwin. The first and obvious result of the first table is, with only one entirely antagonistic exception, the most complete demonstration of the truth of Wallace's suggestion, that a highly conspicuous appearance would be found to be accompanied by some unpleasant attribute. The exception is very remarkable, as the larva is so highly coloured, and I think the total results of all the experiments will justify us in concluding that the larva of *D. euphorbiæ* is unpleasant to some as yet unknown foes, and in all probability that it has been recently distasteful to a larger number. As to the results which bear upon my own suggestion, it must be observed that the only considerable support is to be expected from the columns of experiments under my name, because the other observers did not enter upon the investigation with this object in view, and therefore did not test whether a distasteful form would be eaten when other food was withheld. It will, however, be found that when this test was applied, in nearly all cases the unpleasant larvæ were either swallowed, or a most determined attempt was made to eat them. And there is some incidental support in the other experiments also; for in many instances the larvæ were "tasted" before being rejected, and in other cases even stronger confirmation is forthcoming, when the larvæ were eaten, although "not exactly relished" (Weismann). Since the above was written, Jenner Weir's experiments in 1886 have been included, and these strongly confirm my own observations.

It may be taken as proved that the continued spread of some distasteful form and the corresponding diminution in edible species would lead to the former becoming the prey of insect-eating Vertebrates; for a point would ultimately be reached, as it was reached in many of my experiments, when hunger would become a stronger stimulus than those lesser prejudices in which a species can very well afford to indulge while palatable food is abundant. This prejudice against peculiarities in taste having been overcome in confinement, there is nothing in the conditions of natural life which could prevent the same result from being reached, as doubtless it has been reached, again and again. A comparison of all experiments of this kind ever made with insects will show that the likes and dislikes of insect-eaters are purely relative, and are manifested to a marked extent when they are offered a variety of insects, even when obviously

TABLE II.—*Larvæ which only become*

Species of Larva.	Method by which rendered conspicuous.	Unpleasant attribute real or imaginary.	Results of	
			A. Weismann.	Lady Verney.
Chærocampa elpenor.	Larvæ brown, sometimes green. When approached, the anterior part of the body is distended, and resembles a serpent-like head (of the Cobra type), while the real head is drawn in. Two pairs of large eye-like marks are seen by an enemy approaching from above or the side, while another pair meet an enemy coming from the front, and these last are modified in the terrifying attitude out of other markings. (Poulton, Trans. Ent. Soc. Lond. 1886, pt. ii. p. 154 &c.)	Suggested danger.	A tame Jay ate the larva at once; Sparrows and Chaffinches (wild) were frightened by it, and would not come near the seed-trough in which it was placed; Fowls were evidently frightened, but in the end cautiously attacked it, when it was soon eaten.	Refused by small birds, which were evidently frightened by it, and would not come near a tray with crumbs on it, on which the larva had been placed. ('Good Words,' 1877, p. 838.)
Cerura vinula.	Green and purplish brown. When attacked, the head is drawn in and a bright red margin inflated, with two intensely black marks on it in the appropriate position for eyes; this terrifying face is turned towards any point at which the larva is touched; also pink whips are swiftly protruded from the two prongs in which the body terminates.	Terrifying aspect; the whips might be thought to be stings; the larva also ejects strong formic acid to a considerable distance. (Poulton, Trans. Ent. Soc. Lond. 1886, pt. ii. p. 157.)	Devoured by *L. viridis.*	.....
The phytophagous hymenopterous *Crœsus septentrionalis.*	Green, orange, and black. Gregarious; but not conspicuous until approached; then *most* conspicuous, all individuals whipping about with the abdomen and everting the ventral glands.	Many median ventral glands everted on approach of enemy, and producing a most unpleasant smell.	.....	....
A phytophagous hymenopterous larva, probably *Nematus ribesii.*	Green, with yellow and black markings. Gregarious, becoming conspicuous when approached, as in the last species, but without ventral glands.	? Taste or smell. Proof lies in what follows.	.....	.....

conspicuous when approached and detected.

Experiments.		How far evidence supports Wallace's suggestion.	How far evidence supports Poulton's suggestion.
J. Jenner Weir.	E. B. Poulton.		
.....	.....	Complete support. It would have been very interesting to have also experimented with the Lizards.	Complete support. The working of a counter principle is well seen—the uncertainty of the birds, their evidently half-detecting suspicion, and finally the trial which soon proves the imposition; all this shows the danger of reliance on such a mode of defence.
.....	.....	It would be interesting to also try Birds and other smaller Lizards. This experiment alone opposes suggestion.	Support, if it be found that the appearance is really terrifying to enemies, and yet that the Lizard ate the larva through hunger.
.....	Eaten at one time by nearly all Lizards freely; at another seized without suspicion, but abandoned by *L. muralis*, although a very hungry one was seen to eat the larva, which it evidently disliked.	Support; for the unpleasant qualities certainly produced effect in some cases.	Strong support from the behaviour of the Lizard, which ate the larva reluctantly, although disliking it, because it was hungry.
Refused by Lizards.	Mr. Butler tells me that these larvæ were supplied to the young of the Great Tit by the parent birds. On the other hand, Rev. G. J. Burch tells me that chickens pecked at the larvæ, but rejected them, and that the hen warned them against such food.	Support, from the behaviour of the Lizards and from Mr. Burch's observation.	It is probable that they would have been eaten, like the *Crœsus*, if the Lizards had been very hungry. Mr. Butler's birds appeared to relish the larvæ.

TABLE III.—*Not Inconspicuous Larvæ, which are*

Species of Larva.	Method by which rendered more or less conspicuous.	Unpleasant attribute.	Results of	
			J. Jenner Weir.	A. G. Butler.
Papilio machaon.	Green, black, and orange. "A striking appearance" (*Weismann*). Granting that this is so, when the larva is looked at alone I think that its colours harmonize well with its umbelliferous food-plants. However, when disturbed the pinkish-red everted glands do render it conspicuous; but this is *after* discovery.	A pair of dorsal prothoracic glands, everted when an enemy approaches, and causing a most penetrating odour like "decaying pine-apple" (*Buckler*); especially noticed in fourth stage.	.....	.....
Arctia caja	Black, with very long grey and brown hairs. Freely exposed on dead nettle, &c., although the colour is not such as to at once attract attention.	Jenner Weir thinks that "flavour is nauseous" and that the hairs act as a warning. Nevertheless I am assured that the shorter hairs are irritating (*W. Cole*).	Disregarded by all the birds.	.....
Phragmatobia fuliginosa.	Smoky brown, with brown hairs. Freely exposed on dock &c.; as above, it is not truly conspicuous.	Evidence, as far as it goes, against there being any unpleasant attribute, but only tried with Lizards.	.....	Devoured by *L. viridis.*
Spilosoma menthastri.	Brown, with long brown hairs. Freely exposed on all low plants; as above.	In this case much evidence for the larvæ having unpleasant taste. Jenner Weir thinks hairs are warning.	Young and comparatively hairless; tasted and refused by many birds; disregarded by all when older and very hairy.	.....
Lasiocampa rubi.	Black and brown, with long brown hairs. Freely exposed on heather &c., as above; more conspicuously coloured with black and yellow bands when younger.	I believe that there is evidence for the hairs having irritating properties.	.....	.....
Lasiocampa quercus.	Brown and yellow, and comparatively conspicuous when young; black with white marks and brown and grey hairs when older; exposed but not conspicuous on hawthorn.	I believe that there is evidence for the hairs having irritating properties.	Disregarded by all the birds.	.....
Odenestis potatoria	Blue-grey, black, and orange; tufts of white hairs; freely exposed on grasses. Easily seen, but does not attract attention.	The hairs are certainly irritating, although it takes some time to affect the hands.	Disregarded by all the birds.	.....

not Nocturnal and which do not conceal themselves.

Experiments.		How far evidence supports Wallace's suggestion.	How far evidence supports Poulton's suggestion.
A. Weismann.	E. B. Poulton.		
Two full-fed larvæ quite unnoticed by *L. viridis*; they finally pupated on side of Lizard's cage.	.....	As offered to the Lizards the larvæ were no doubt conspicuous, and so the experiment supports the suggestion. It is possible that some notice may have been taken by the Lizards, but that they were repelled by the penetrating smell.	No evidence.
.....	.....	Favourable to the suggestion, for the larva is certainly not well-concealed.	No evidence.
.....	.....	We cannot say more than that it does not oppose suggestion.	No evidence.
.....	... .	Conclusion as in case of *A. caja*.	No evidence.
Offered to *L. viridis* when young and resembling *E. jacobææ* (having dark and yellow bands). Nevertheless eaten after cautious tasting.	.....	Thus eaten when young and more conspicuously coloured; no evidence when older. So far as it goes, the evidence is rather antagonistic.	No evidence.
.....	Disregarded by the Lizards. (Adult form of larva.)	Neutral as far as the adult larva is concerned (no evidence from the younger form).	No evidence. Only one larva made use of with Lizards.
.....	Disliked, but eaten by hungry *L. muralis*, and probably by *L. viridis* also.	Conclusion as in the case of *A. caja*.	Strong support from behaviour of hungry Lizards.

distasteful species are carefully excluded from the diet. Thus Butterflies and Moths are freely eaten by Lizards (see Appendices); but I am sure that they are not really enjoyed in the same way as when a Housefly or a palatable Caterpillar is offered to them. This is doubtless because the imagos of Lepidoptera are dusty, unsatisfactory things to eat, with such a small proportion of body in which the real nutriment and taste is contained, and so large an expanse due to the dry membranous wings with their scaly covering. In this respect the Butterflies contrast unfavourably (as food) with the Moths, and the latter are certainly preferred (when both are palatable in other ways). The same preference is manifested by Frogs (*Hyla arborea*) with even greater force; there is a most extraordinary difference in the behaviour of such a Frog in the presence of a Housefly or of a Butterfly respectively, and in fact the latter is often disregarded. Of course birds are in a different position as regards such insect-food, for they at any rate very generally pick off the unpalatable parts before eating a lepidopterous imago (Jenner Weir); and with them it is common to witness all the signs of an intense desire for these insects, especially Moths. Birds can similarly largely remove the unpleasantness due to larval hairs, as was seen in the case of *O. antiqua* (Table I.). We should doubtless see evidence for the existence of such nice discrimination between the relative palatabilities of various insects, in the case of all insect-eaters, if our observations were sufficiently numerous and minute; but it must be quite clear that the preferences cannot be always satisfied, when we remember the extent and keenness of competition. In this country it is hard to realize the excessive abundance of reptile life, chiefly among the Lizards, which obtains even so near to us as the south of Europe, and which almost entirely depends upon the insect fauna for food. Almost every step along an Italian road startles several Lizards on the road-side wall or bank; and it must be perfectly clear that under such circumstances it is quite impossible for all to be served with the food which is most appreciated. We see rather the very conditions which must render the acquisition of an unpleasant taste together with the correlative "warning" colours, an exceedingly hazardous mode of protection, if assumed by more than a small proportion of the species constituting the insect fauna of such a country. For in so great a press of competition among the innumerable insect-eaters, we may feel sure that some at least would be sufficiently enterprising to make the best of unpleasant food, which has at least the advantage of being easily seen and caught. And such a conclusion will, I think, be confirmed by a study of the tabulated details. It must be admitted that Wallace's suggestion, with its experimental proof, has taken a most important place among the principles which deal with the infinitely complex and ever-changing relations which obtain between the most widely separated no less than between the most allied members of the organic kingdom. But it is no less true that the principle carries with it its own compensating principle, which will come into operation precisely as the former advances to the possession

of undue influence and thus throws out of adjustment the preexisting condition of comparative equilibrium.

Another conclusion which is demonstrated very completely by the tables is that a Caterpillar may be eaten by one insect-eating Vertebrate although refused by another. I believe, however, that the acquisition of an unpleasant taste and of conspicuous colours appealed, at any rate at first, to a large number, probably all, the vertebrate foes; for if this were not so, if the species became unpalatable and conspicuous to (say) half its enemies, and became conspicuous but remained palatable to the remainder, it seems only reasonable to conclude that immunity from the attacks of one set of foes would be counterbalanced, or perhaps more than counterbalanced, by the facilities afforded to the other set. On this account and for other reasons which will be given below, I think it probable that the differences observed between the enemies of insects in this respect are of recent date as compared with the acquisition of this mode of protection, and have arisen out of the great competition for food; but in most instances the change of habit has not become so far confirmed that the previously distasteful food is eaten with avidity and pleasure. The first table of highly conspicuous larvæ (including *Crœsus* and *Nematus* from the second table) can be shortly analyzed to show in it the various stages of transition from the most utter disregard to the opposite extreme of conduct, indistinguishable from that observed when the larvæ are known to be relished. The intervening stages are furnished by the details given by the different observers, and are described in the headings of the vertical columns between those numbered I. & V. (see page 212).

It must be remembered that these analyses represent a comparison between the results of experiments carried out under different systems and with the use of an incomplete number of Vertebrates in all cases. Hence many of the insects would doubtless have to be shifted into other columns after being offered to other Vertebrates, or to those actually employed, if it were certain that they were thoroughly hungry. Allowing for this, however, the analyses provide us with numerous instances of transition through all conditions of failure in the protective efficacy of the method we are discussing. At the same time one can see at a glance the relative behaviour of different insect-eaters as far as they have been tested in the case of each larva.

Jenner Weir's suggestion that the hairs of certain larvæ act as a warning of other unpleasant qualities can also be tested by the examination of the former tables. There are altogether fourteen larvæ which may be called hairy, out of a total of twenty-seven (omitting the two terrifying species). Of these, two (*L. rubi* and *P. fuliginosa*) were eaten, as far as any observations are recorded; one of the former and five others (*L. rubi*, *L. quercus*, *L. pini*, *P. auriflua*, *A. caja*, and *O. potatoria*) are either known to possess irritating hairs or are believed to possess them; as many as five are gregarious (*V. io*, *V. urticæ*, *P. bucephala*, *E. lanestris*, *C. neustria*), and this habit, together with the colour, is by far the most important factor

B.=Birds, F.=Frogs, L.=Lizards, S.=Spiders.		I. Disregarded.	II. Tasted, and then rejected.	III. Eaten when very hungry, and evidently much disliked.	IV. Eaten, but not relished.	V. Eaten with avidity.
A. Disregarded by all Vertebrates as far as experiments have been made at present.	*V. io, A. filipendulæ, D. cæruleocephala, H. defoliaria.*	B.				
	D. galii, P. brassicæ	L.				
B. Disregarded by some foes; tasted and rejected by others.						
C. Disregarded by some foes, but eaten, in some cases with relish, by others.	*C. neustria*	B., L.	L.	L.		
	E. jacobææ	L.	L.	?L.		
	A. grossulariata	B.,L.,F.	F.,S.,L.	L.		
	P. bucephala	L.	L.	L.		
	O. antiqua	B.	...	...	B.	
	E. lanestris	B.	...	...	L.	
	P. auriflua	B., L.	L.	...	...	?B.
	C. verbasci	B.	...	...	...	?B.
	V. urticæ	B.	...	...	...	L.
	N. ribesii	B., L.	B.	...	...	B.
D. Disregarded by no species of enemy.	*C. septentrionalis*	...	L.	L.	...	L.
	H. wavaria	...	F., S.	...	...	B.
E. Eaten with more or less pleasure by all the species of enemy on which experiments have been made.	*L. pini*	...	...	...	L.	
	D. euphorbiæ	...	...	...	...	B., L.

Similarly analyzing the third table, we find the following results:—

		I.	II.	III.	IV.	V.
A.	*P. machaon*	L.				
	A. caja, S. menthastri (old)	B.				
	L. quercus	B., L.				
B.	*S. menthastri* (young)	B.	B.			
C.	*O. potatoria*	B., L.	L.	L.		
E.	*P. fuliginosa*	...	...	...	...	?L.
	L. rubi	...	..	...	...	?L.

in producing a conspicuous appearance, although it may be admitted that the hairs do render subordinate assistance; of the two remaining larvæ, one is brightly coloured (*O. antiqua*), although the hairy tufts are in this case very important factors, while for *S. menthastri* no other suggestion except that of Jenner Weir has yet been made. In some of these larvæ the effective colours are chiefly on the hairy covering, and the latter practically makes up the whole appearance. Furthermore in the last species there is evidence (Jenner Weir) that the insect is disliked for some quality other than the presence of hairs. It seems probable that the hairs of larvæ possess irritating qualities to a much greater extent than is commonly supposed; but it is also likely that the hairy covering may be of direct value to the organism in other ways, some of which doubtless remain to be discovered. (Is it not likely that some tactile or other terminal organ of the nervous system may be in relation with hairs or bristles?) Of course it is well known that hairs are often exceedingly important in defending the insects by the converse method of a protective appearance (an extreme instance of this is afforded by the larva of *Acronycta leporina*, see Trans. Ent. Soc. Lond. 1886, pt. ii. June, p. 160).

Prof. Meldola has kindly looked through the proof-sheets of this paper, and has suggested to me that the probable original significance of the hairy covering was protection from injury after falling from the food-plant. The suggestion is strongly supported by the habits of the majority of hairy larvæ.

Any further considerations which arise out of the tables given above are better deferred until after an examination of similar instances in forms other than the larvæ of Lepidoptera.

II. *Brightly coloured or conspicuous Insects (other than Larvæ).*

Under this heading I have only included such species as have been actually subjected to experiment. There are a very large number of additional species from many groups of insects which doubtless belong to this category; but as they have never been brought to the experimental test, they are excluded from consideration on the present occasion. An extended list will be found in Wallace's 'Contributions to the Theory of Natural Selection' already referred to (The essay on "Mimicry and other Protective Resemblances among Animals"). In most of the instances given by Wallace, we may feel confident that the test would prove satisfactory, especially as the author shows that in many cases the conspicuous form is mimicked by one or more species belonging to totally different groups, which accompany the former in its range and which, nearly always, keep in a small minority. Such facts render it in the highest degree probable (in fact make it nearly certain) that the mimicked species possesses some exceptional advantage in the way of inedibility or otherwise—some unpleasant peculiarity which confers upon it a more or less complete immunity from the attacks of the Vertebrate foes of its class. But in the present paper I am rigidly limiting myself to instances

which have been actually tested, and it is much to be regretted that experimental investigations have not been further extended and recorded in greater detail. The results of the tables of larvæ given above have been, in a very small proportion of cases, so directly contrary to *à priori* expectation that I do not feel confident in bringing forward any instances which have not been tested, although I feel sure that the vast majority of them would yield favourable results. I cannot, therefore, in this paper accept as satisfactory the purely negative evidence that insect-eating Vertebrates have been often seen to catch and eat insects of various kinds, but have not been seen to catch at the same time and place certain highly coloured species which were abundant and slow-flying. At the time when Bates and Wallace first made public their most important conclusions as to the meaning of conspicuous coloration and the true significance of mimicry, it was quite right that evidence of all kinds should be brought forward; but after the lapse of twenty years, we may fairly expect that conclusions which are so important in Biology shall have received the most abundant and complete experimental proof. And I know that lack of detail in the proofs which have been afforded, and the fact that a large part of the evidence brought forward is still founded on mere surmise (however probable may be the result of an actual test), have prejudiced the conclusions in the minds of many distinguished biologists, who have come to look upon the whole subject with an undeserved suspicion.

I cannot find any record of actual experiments conducted upon the well-known and conspicuous Heliconians and Danaids, and therefore I do not include them in the following list. There is, however, an observation of Meldola's which is of the nature of demonstration, and which is so interesting that I quote it in his words:—"It appears that the nauseous character of these . . . . butterflies is to a certain extent retained after death, as I found that in an old collection which had been destroyed by mites, the least mutilated specimens were species of *Danais* and *Euplœa*, genera which are known to be distasteful when living and to serve as models for mimicry, see Proc. Ent. Soc. Lond. 1877, p. xii." (Meldola's editorial notes to his translation of Weismann's Essays above referred to, p. 337). This observation (since confirmed by J. Jenner Weir, 'Entomologist,' vol. xv. 1882, p. 160) has the same kind of interest as that of Butler upon spiders, drawing attention, as it does, to the possession of a peculiar taste or smell which is recognized as nauseous by animals as widely separated as the mites and spiders are from lizards and birds. And such a consideration enforces the conclusion previously arrived at from other evidence, that when certain insect-eaters neglect the attributes which are respected by others, we see the results of an "acquired taste" produced in the first instance by hunger, and not by an obedience to the dictates of an eccentric preference for what is very universally regarded as disagreeable.

Since the above was written, my friend and pupil Mr. E. A.

Minchin has called my attention to some experiments made by M. de Nicéville upon the imagos of Acræinæ &c. (Butterflies of India, Burmah, and Ceylon, vol. i. part ii. p. 318). "M. de Nicéville has experimented with the carnivorous *Mantis* on many of the Butterflies believed to be offensive to birds, and he has found that *A. violæ* is the only Butterfly which all the species of *Mantis* he has experimented with refuse to eat."

One other consideration remains to be partially discussed before giving the list of experiments. The meaning of conspicuous coloration may be said to be clear and definite in the case of larvæ, being only capable of the explanation that it is of value for protective purposes. But in the perfect forms the other explanation of colour is always possible, *i. e.* its use in courtship, and, as a consequence, its growth from small beginnings and its gradual perfection by sexual selection. By what criterion, then, is it possible to judge of the meaning of bright and conspicuous colours in any particular instance? In the first place, the brilliant tints due to sexual selection alone rarely usurp the whole surface of an insect, and there are certain parts (exposed in the protective attitude of rest) in which we expect to find such brilliant tints replaced by the (usually) sober colours which harmonize with the environment. For instance, this is well known to be the case with the uppersides of the upper wings in most moths, and with the undersides of both wings in nearly all butterflies. If, therefore, such exposed parts are conspicuously coloured, strong presumptive evidence will be afforded for the explanation of the colour as belonging to the "warning class." Another test is found in the mode of flight, which may be expected to be such as will clearly display the colours no less than when the insect is at rest. The question is no doubt complicated by the two kinds of coloration running into each other. Thus Wallace has shown that the shapes and colours due to sexual selection may run riot in localities (certain islands) where enemies are largely excluded by barriers, and in the same way the brilliant colours of dangerous or nauseous insects may perhaps be sometimes explained by equal immunity, although due to other causes. But a conspicuous appearance gained in this way will be always liable to be used for an entirely different object as "warning coloration." But if such a change of use took place, we should expect some change of pattern or some new combination of colours, for this reason, that "warning colours" have one meaning which is not associated with sexual colours, *i. e.* the production of a conspicuous appearance and the more or less complete subordination of everything to this end. Nevertheless it is almost certain that the appearance of any species, however specialized for other ends, possesses sexual significance, and appeals as an adornment to the modified taste of the individuals concerned; and we have a rough criterion of the extent of the modification in taste, when we compare such appearances with those which possess a sexual value alone, which are concealed except during flight and which are especially displayed during courtship. Prof. Meldola has recently drawn my attention to an observation of

Darwin's which enables us to point towards the purely sexual value of one factor in the appearance of certain butterflies; and by the same kind of observation it is likely that increasing stability will be given to the whole theory of sexual selection. Darwin noticed that the magnificent surface-colours which exist on many tropical butterflies, and which change with the position from which the insect is observed (being probably due to diffraction), become most brilliant when they are seen from the front, and at an angle which corresponds with that at which they would be seen by the female as the male butterfly approaches her.

As a further test of the "warning" value of certain colours, we can use as a comparison the colours and patterns of certain larvæ which are known to be "warning" only, or which at any rate cannot be sexual. After giving the list and the experimental details, I shall attempt to show that there are certain combinations of colour, and sometimes even certain patterns, which are generally distinctive of "warning" as apart from sexual coloration. And such differences of type are to be expected; for the two systems of coloration appeal to a different class of animals and appeal to a different sense. The "warning" colours of insects appeal to a *Vertebrate's* sense of what is *conspicuous*; the sexual colours appeal to an *Invertebrate's* sense of what is *beautiful*. And it is one of the most remarkable facts in the study of comparative psychology that our own sense of what is beautiful entirely coincides with that of an insect, so that the difference in the two types of coloration depends entirely upon the *sense* alluded to above, and has probably no reference to the class of animals in which the sense exists. For, if we had no knowledge of the use and meaning of the colours of insects, we should all agree in maintaining that certain colours and patterns (which we now trace to the action of sexual selection) comprise all that is beautiful in the appearance of this class of animals, and we should draw a sharp line between these and other combinations of colour which we now recognize as possessing an entirely different significance.

In the following instances it is unnecessary to enter upon any preliminary account, as the table contains all the details which I can find recorded. Of course this list must contain any cases (if tested) in which a conspicuous appearance is believed to be due to "mimetic" resemblance to another species protected by possessing some unpleasant attribute. I much regret that hardly any of these most interesting cases have been used for experiment (see Table IV., pp. 218–223).

Looking at this fourth table, we find that the theory of warning colours is again confirmed in the most marked manner. Unfortunately the extremely interesting "mimetic" cases still lack the necessary experimental demonstration; although the intimidating larvæ of *C. elpenor* and *C. vinula* are really mimetic of vertebrate appearances, and the former has been shown to be attended by a considerable amount of success. The only "mimetic" form in this last list is *Sesia fuciformis*, and in this case the mimicry is

exceedingly imperfect, while very perfect protection is gained in other ways. In fact I have suggested above that the species is not now "mimetic" at all, but retains two points of an ancestral condition in which it actually derived shelter from the reputation possessed by many Hymenoptera, these being (1) a structural point—its transparent wings, and (2) a habit—its diurnal flight. If this view be correct the species should be moved into the table given below of the results of experiments upon insects protected by evading their enemies, and *there* it would add to the instances which support Wallace's converse suggestion, that such insects will be found to be eaten just as the class we are discussing are generally refused. I have placed the species in the fourth table in deference to Wallace's opinion on the kindred species *S. bombyliformis*, which it closely resembles; but I believe that the place of both species should be below. I made several attempts to obtain the imagos of *Sphecia apiformis*, in order to offer these to my Lizards; for this species certainly does suggest a stinging Hymenopterous insect in the most remarkable way; but the attempt was unsuccessful. *S. bembeciformis* is equally well suited for experiment, but even more difficult to obtain; I hope, however, to be able to experiment with one or both species in the course of next summer.

It is noteworthy that (excluding *S. fuciformis*) there is probably no instance in this list which proves a difficulty in the way of Wallace's suggestion at all equal to that raised by the larva of *D. euphorbiæ*. For the pupa of *A. grossulariata* was not swallowed, but only well bitten by a very hungry lizard, and although the imagos of *S. lubricipeda* and *P. auriflua* were eaten (also by very hungry lizards in the former case), it cannot be asserted that they were eaten with relish; and, further, the experiment should be repeated with Birds and other species of Lizards. In all other cases the insects were refused by at least one of the animals to which they were offered. The comparison between the treatment received by Bees (described below) and Wasps, together with a comparison between their appearances, is strongly in favour of Wallace's suggestion. It now remains to analyze the list in the same manner as was adopted before, showing the transition of conduct observed (see Table, page 224).

Comparing the three analyses of all experiments ever conducted upon presumably nauseous or dangerous insects, omitting *S. fuciformis* and including *C. elpenor* and *C. vinula*, we find that out of a total of 44 cases which have been tested 13 were entirely disregarded; but this number includes *P. machaon*, which I believe ought to be placed below under forms chiefly defended by protective resemblances, and also *S. menthastri* (larvæ, which were tasted in the youngest stages). Furthermore four species (including the two just mentioned) belong to Table III., containing larvæ which can hardly be called conspicuous. Hence, omitting this table, the number is reduced to 9 cases out of a total of 37; and of the 9, not a single species has been offered to more than one out of the three groups of

TABLE IV.—*Bright-coloured or Conspicuous*

Species and Stage.	Method by which rendered more or less conspicuous.	Unpleasant attribute, real or suggested, in mimetic forms.	Results of	
			J. Jenner Weir.	A. G. Butler.
Pupa of *Abraxas grossulariata.*	Black, with yellow bands; contained "in a very slight and perfectly transparent cocoon" (*Newman*).	? Taste or smell. Proof lies in what follows.	.....	.....
Imago of *Anthrocera filipendulæ.*	Blackish green and red. Rests very conspicuously on flowers &c.; flight not rapid, and by day. So abundant locally as to be almost gregarious. The bright colours are well seen at rest and in flight; very sluggish and easily caught; often feigns death when captured.	? Taste or smell. Proof lies in what follows.	"Unwillingly eaten:" Jenner Weir thinks because the birds in confinement get fewer insects than when wild, and so will eat forms which they would reject if well supplied with this food.	Always refused by *L. viridis* after having been seized.
Imago of *Sesia fuciformis.*	Wings transparent, with brown margin; body various shades of brown. Flight by day *very* rapid, and insect seldom seen at rest. Its claim here depends on its somewhat Hymenopterous appearance: the closely allied *S. bombyliformis* "resembles the male of the Humble-Bee (*Bombus hortorum*)" (*Wallace*).	The suggestion of a sting, according to some authorities.	.....	.....
Imago of *Porthesia auriflua.*	Almost all the surface, seen at rest, is white; there are also a few small black patches on the fore wings, and the body ends posteriorly in a conspicuous yellow tuft. Flight weak in the evening, when the Moth is very conspicuous, appearing white; at rest it is also extremely conspicuous.	There may be an unpleasant taste or smell, but there is at present no experimental proof of this.	A single imago eaten by the Lizards.	.....

Insects (other than Larvæ).

Experiments.		How far evidence supports the theory of "warning" and "mimetic" colours (Bates and Wallace).	Bearing of evidence on Poulton's suggestion, as before.
A. Weismann.	E. B. Poulton.		
.....	One was placed in cage of very hungry *L. muralis*, and was crushed and most of the fluid contents extracted and probably eaten; however, palatable pupæ were swallowed as a whole. This pupa was untouched at first.	Strong support, for if palatable it would have been treated very differently.	Strong support.
.....	.....	Strong support, from the reluctance of Birds and rejection by Lizards.	Strong support in Jenner Weir's explanation of the Birds' behaviour, and some support in the Lizard's attempts.
.....	One specimen eaten by *L. muralis*; no apparent hesitation or caution in capture.	At first seems to be a difficulty; but I have always thought that the suggested resemblance is very imperfect, and perhaps a remnant of a former more perfect mimicry, reliance being now placed on powerful flight and concealment during rest.	No evidence, the insect being palatable and in this instance not terrifying.
.....	.....	Insufficient evidence; but opposed to the theory as far as it goes.	No evidence, unless it should be proved to be a nauseous insect.

TABLE IV.

Species and Stage.	Method by which rendered more or less conspicuous.	Unpleasant attribute, real or suggested, in mimetic forms.	Results of	
			J. Jenner Weir.	A. G. Butler.
Imago of *Spilosoma menthastri.*	Wings creamy white, with black dots; body yellow, with black dots. Very conspicuous at rest or in flight (slow; evening); often feigns death when captured.	? Taste or smell. Proof lies in what follows.	Eaten reluctantly by Robin and Reed-Bunting, the latter after rejecting it at first. Tasted and rejected by Yellow-Hammer; refused by Bullfinch and Chaffinch.	.....
Imago of *Spilosoma lubricipeda.*	Buff, with black spots. Very conspicuous at rest or in flight (slow; evening); often feigns death when captured.	? Taste or smell; but there is at present no experimental proof of this.	.....	.....
Imago of *Euchelia jacobææ.*	Fore wings very dark brown, almost black, with red spots and stripes; hind wings red with black margin; body black. Most conspicuous at rest, or especially in its weak flight by day.	? Taste or smell, or very probably from being indigestible.	Disregarded for some time, but eventually reluctantly swallowed after the removal of the wings. Same suggestion as in case of *A. filipendulæ.*	.....
Imago of *Abraxas grossulariata.*	White, black, and yellow. Very conspicuous at rest or in its slow flight by day and in evening. Often feigns death when captured.	? Taste or smell. Proof lies in what follows.	Refused by Lizards, although seized on one occasion.	"Greedily devoured" by Frogs. (I think that this must be a mistake)
Imagos of Malacoderms of the genus *Telephorus*, sp. ? (Coleoptera).	Black and red. Very conspicuous at rest or in flight (diurnal); easily caught. Elytra soft and no protection. Common English species called "soldiers and sailors."	? Taste or smell. Proof lies in what follows.	Disregarded by all the birds. (Quoted by Wallace.)	.....

(*continued*).

Experiments.		How far evidence supports the theory of "warning" and "mimetic" colours (Bates and Wallace).	Bearing of evidence on Poulton's suggestion, as before.
A. Weismann.	E. B. Poulton.		
.....	.....	Strong support. Also confirmed by Stainton, who offered it to Turkeys, with a large number of protectively-coloured Moths, all of which were eaten, while the *S. menthastri* was always rejected after being examined.	Strong support, especially in the reluctant way in which it was eaten by Robin &c. See Jenner Weir's explanation in case of *A. filipendulæ*.
.....	Eaten at once by hungry *L. muralis*.	So far as it goes, against suggestion; but not tried with sufficient number of enemies, nor with plenty of other food.	No evidence, unless it should be proved to be nauseous; then this experiment would strongly support suggestion.
Always refused by *L. viridis*.	Two specimens eaten successively by the same Frog, and therefore it would seem not to be nauseous to this species. Next day the Moths were found in the case, having been rejected presumably because of indigestibility.	Strong support.	Strong support in Jenner Weir's explanation as above. In the case of the Frog also hunger very likely caused the insect to be taken, although not retained.
.....	Refused by *L. muralis* after biting, although very hungry.	Support from the behaviour of Lizards; the other evidence must, I think, be mistaken.	Support in that the Lizards were induced to bite it severely.
.....	.....	Strong support.	No evidence.

TABLE IV.

Species and Stage.	Method by which rendered more or less conspicuous.	Unpleasant attribute, real or suggested, in mimetic forms.	Results of	
			J. Jenner Weir.	A. G. Butler.
Imago of *Chrysomela populi* (Coleoptera).	Chief colour red, due to elytra: the other parts seen are a metallic lustrous blue-black.	"Strongly smelling" (*Weismann*).	.....	.....
Coccinella septempunctata (Coleoptera).	Exposed surface red with black spots. Very conspicuous and easily caught; flight diurnal.	They have a very unpleasant smell. They "can emit fluids of a very disagreeable nature" (*Wallace*).	.....	.....
Coccinella bipunctata (Coleoptera).	Exposed surface red with two black spots. Very conspicuous and easily caught; flight diurnal.	They have a very unpleasant smell. They "can emit fluids of a very disagreeable nature" (*Wallace*).	.....	.....
Vespa vulgaris.	Queens and workers made use of: colours black and yellow. Very conspicuous; powerful flight, but of use for obtaining food and catching prey rather than for escaping enemies.	Sting.	.....	.....
Bombus terrestris, *B. lapidarius*, &c.	Other common species also made use of. The insects are generally conspicuous, with bands of light colour (often yellow) on a darker ground (often black). Their size also attracts attention, while their flight is clumsy and heavy, and they do not rise quickly when at rest.	Stings.	*Bombus* ? sp., killed, but not swallowed, by *L. viridis*.	*Bombus terres* is eaten by *L. viridis*, after cautious disablement, as in the case of Bees. Only eaten when hungry.
Nomada marshamella.	Very conspicuous, with black and yellow bands.	Sting.	.....	.....

(*continued*).

Experiments.		How far evidence supports the theory of "warning" and "mimetic" colours (Bates and Wallace).	Bearing of evidence on Poulton's suggestion, as before.
A. Weismann.	E. B. Poulton.		
Always rejected by L. *viridis*.	.....	Strong support.	No evidence.
.....	Refused by Frogs without tasting; also by Lizards. Miss Cundell tells me that *Hyla arborea* will eat Ladybirds in the winter when food is scarce.	Strong support.	Strong support from Miss Cundell's observation.
.....	Refused by Frogs without tasting. See Miss Cundell's observation quoted above.	Strong support. Wallace also says of the Coccinellidæ, to which family this and the last species belong:—"Certainly rejected by some birds;" but no details are given.	Strong support from Miss Cundell's observation.
.....	Three Frogs in succession caught one queen Wasp and then released it very quickly, and after that it was untouched. Lizards would not touch it, but watched it narrowly.	Strong support. Romanes also told me he had seen a Spider capture a Wasp, and its great caution in the process was a further support, as also is the fact that Spiders generally release Wasps from their webs.	The Frogs went as far as or farther than could have been expected.
.....	*Bombus lapidarius* eaten by *L. viridis*, but I have not witnessed the method. Refused on many occasions.	Support, upon the whole; they would certainly not have been touched by the Lizards if there had been abundance of other food.	Strong support for an analogous suggestion for insects protected by stings instead of by a nauseous taste.
.....	Untouched by any of the Lizards.	Strong support.	This seems to indicate that the fear of a sting is very strong; for when the insects are too active to be killed without stinging (also the case with Wasps), they are not touched by the Lizards.

		I. Disregarded.	II. Tasted and then rejected.	III. Eaten when very hungry, and evidently much disliked.	IV. Eaten, but not relished.	V. Eaten with pleasure.
A.	*Chrysomela populi*	L.				
A.	Malacoderms of the genus *Telephorus*	B.				
A.	*Nomada marshamella*	L.				
B.	*Vespa vulgaris*	L., F.	F.			
C.	*A. filipendulæ*	L.	...	B.		
C.	*A. grossulariata*	L.	L.	...	...	F.? (I think a mistake).
C.	*S. menthastri*	B.	B.	B.		
C.	*E. jacobææ*	L.	...	B.	...	F. (at the time).
C.	*Bombus terrestris, B. lapidarius,* &c.	L.	L.	L.		
C.	*Coccinella bipunctata*	F.	...	F.		
C.	*Coccinella septem-punctata*	F., L.	...	F.		
D.	.....	...	...	...	...	...
E.	Pupa of *A. grossulariata*	...	...	L. or II.		
E.	*S. lubricipeda*	...	...	L.? or IV. or V.		
E.	*S. fuciformis*	...	...	...	...	L.
E.	*P. auriflua*	...	...	...	...	L.? or IV. or III.

insect-eaters. Again, only one species out of the 9, viz. *Nomada marshamella*, always remained untouched by very hungry animals when other food was withheld; and we can only surmise as to what would have been the results if the other 8 had been similarly tested. It is, however, quite certain that many of them would have failed. This is, indeed, proved by the following figures:—Out of the 37 cases 15 were exposed to this rigid test, *i. e.* the species in the columns under my name in Tables I., II., and IV. (excluding *S. fuciformis* and *C. neustria*), and of the 15 only three remained untasted, and of these two have been shown by Miss Cundell to be eaten under certain circumstances.

Looking at all these figures, and especially the last, we can well understand the following objection being urged against Wallace's suggestion. It may be said, the tables, indeed, show that Wallace was right in predicting that an unpleasant attribute would be found to be associated with a conspicuous appearance. That has certainly been proved by the results of a vast majority of the experiments; but of what value is this association when insects are seized, tasted, and rejected in spite of the warning colours which, *ex hypothesi*, are assumed to prevent this very contingency? In the first place, an answer to the objection is found in the very fact that the insects were tasted and rejected to a much greater extent when the vertebrates were thoroughly hungry, for we see that when other food is present the conspicuous insects are, as a rule, untasted. We shall presently see that an inconspicuous but nauseous insect is approached by Lizards in a very different way from one which is conspicuous and nauseous. There was, in fact, strong evidence in the details of some of my experiments, that the vertebrate enemies were well aware that the insects were distasteful, and yet, when exceedingly hungry, did their best, in some cases successfully, to eat them. This was especially seen in the behaviour of the Lizards towards the larvæ of *O. potatoria*, *P. bucephala*, and *Crœsus septentrionalis* in my experiments, and towards the larvæ of *C. neustria*, *A. grossulariata*, and *P. auriflua* in Jenner Weir's experiments; for in all these cases the Lizards made repeated attempts to eat the larvæ, again and again rejecting their prey with every sign of disgust (rubbing the mouth against the cage); and yet in the end the larvæ were reluctantly eaten. I believe, however, that the suspicion with which conspicuous insects are approached results from the strongly impressed experiences of early youth and not from a habit which has become hereditary. In many cases, however, the warning experience may have been gained without tasting the insects; for we have seen that the latter are often protected by smell, which can be perceived from a distance. Excluding these instances, however, the experience of conspicuous nauseous forms must have been gained by actual trial of a large number. I hope to be able to show that it is not necessary for the young insect-eating Vertebrate to actually make trial of every species of unpleasant-tasting insect in its locality, in order to be equipped with an efficient stock of experiences with which to conduct its later life.

Such an education would be somewhat dearly bought; it would be unpleasant to the insect-eater and destructive to the insect. But if, as I shall endeavour to show, there is a superficial resemblance between the colours employed by very different insects, and frequently even a similarity of pattern, we see that a comparatively few unpleasant experiences would be sufficient to create a prejudice against any insect with colours and patterns at all resembling the nauseous forms which have already produced so indelible an impression upon the memory. And thus it is most probable that the conspicuous appearance which astonishes one sense becomes associated in the mind of the Vertebrate insect-eater with the well-remembered effect of other qualities upon other senses. Different Vertebrates vary much in their rates of education. Thus my Frogs were much more stupid in this respect than the Lizards; but then the imperfect memory or limited power of generalization in Frogs is less fatal to insects than it would be in the case of the other Vertebrates; for I do not think that the larvæ were ever injured in the least after having been tasted by these animals. It is therefore probable that the gradual development of warning colours by natural selection was due to the fatalities which followed the experimental tasting of other Vertebrate enemies (especially Birds and Lizards), which inflict incidental injuries during the process of tasting. But the warning appearance having been acquired by such means, the Frogs have certainly taken the opportunity (thus offered to them ready-made and without having themselves contributed towards its existence) to acquire a somewhat limited education. This was seen in the case of the queen wasp (see Appendix II.), which on being placed in the case was tasted by three Frogs out of twelve, but afterwards was untouched for many hours (as far as I was able to observe). A proof of the limited extent of the education is given by Butler, who speaks as if his Frogs repeatedly tried to eat the two species of nauseous larvæ (*A. grossulariata* and *H. wavaria*), seeming only to become suspicious when they had actually made a trial of the insects on each separate occasion. It also seemed to me that my Frogs generally, if not always, ate bees from want of memory or deficient discrimination; for in nearly all cases they were finally rejected. But the experience did not seem to make any difference to the readiness with which the next bee would be seized and again rejected. On the other hand I did not see a ladybird tasted on any occasion. The slight power of discrimination possessed by Frogs was also shown by the fact that they frequently jumped at and seized the dark-coloured ends of the forceps with which I used to introduce insects into their case.

For the tolerably complete demonstration of the principle which I believe has been at work, a far larger number of observations are necessary, while complete confirmation requires experimental evidence with young Vertebrates which have been reared in confinement, so that the whole of their education is under observation. As conducing towards this end, I publish the suggestion with its foundation on the resemblances indicated by the tables given below, which have this

advantage, that they only include insects which have been subjected to actual experiment. Although the tables comprise so few instances, I think that the resemblances of colour and pattern are most remarkable, and hard to explain under any other theory. My suggestion does at any rate point out a very obvious use for the resemblances. The advantages which every conspicuous and nauseous or dangerous species would gain by setting as simple a lesson as possible to the foes of its class, would be so great that there is no difficulty whatever in the supposition that every stage towards convergence in colours and in patterns would have been beneficial, and, as such, would have come under the influence of natural selection. It is to be noted that advantage would accrue in the greater thoroughness of the education, no less than by shortening the process; for a few colours, with a few simple patterns scattered over a number of species, would be remembered more easily than a larger number with a separate pattern in nearly every species.

I am aware that this suggestion is but an extension to the whole group of conspicuous insects of the explanation offered by Fritz Müller to a fact which seemed for a long time an inexplicable difficulty, the undoubted fact that conspicuous butterflies presumably protected in the most complete manner by nauseous attributes, nevertheless mimic each other in the most unmistakable way. Bates, the original discoverer of "mimicry" in the animal kingdom, pointed out these apparently mysterious resemblances in the paper in which "mimicry" was itself explained and illustrated. Wallace looked upon these obscure similarities between protected forms as due to some unknown cause connected with locality.

It remained for Dr. Fritz Müller to explain the difficulties in a paper entitled "*Ituna* and *Thyridia*; a remarkable case of Mimicry in Butterflies" ('Kosmos,' May 1879, p. 100). Arguing from the instance of these two genera, which both belong to protected groups and which resemble each other, Dr. Müller suggested that under these circumstances an advantage would be gained by each of them, because the number of species which must be sacrificed to the inexperience of young birds and other enemies would be made up by both of them instead of by each independently. This paper was translated by Prof. Meldola, and appeared in the 'Proc. Ent. Soc. Lond.' (1879, p. xx). In a subsequent paper by Dr. Müller ('Kosmos,' v. Jahrgang, 1881), the same subject is considered in greater detail, and the results are accepted and expounded by Wallace in 'Nature' (vol. xxvi. p. 86). The mathematical aspect of the subject was, however, inaccurately stated in this last paper, the correct statement being supplied by Mr. Blakiston and Mr. Alexander of Tokio, Japan; the correction being published in letters by Mr. Wallace and Prof. Meldola to 'Nature' (vol. xxvii. p. 481). Subsequently a letter appeared in 'Nature' (vol. xxix. p. 405) from Mr. Blakiston and Mr. Alexander, giving the complete mathematical statement of the advantages gained by each of the protected species. The law is given in these words, "Let there be two species of insects equally distasteful to young birds, and let it be supposed that the

birds would destroy the same number of individuals of each, before they were educated to avoid them. Then if these insects are thoroughly mixed, and become undistinguishable to the birds, a *proportionate advantage* accrues to each over its former state of existence. These *proportionate advantages* are inversely in the duplicate ratio of their respective original numbers, compounded with the ratio of the respective percentages that would have survived without the mimicry."

It had been previously argued that in the case of two protected species which had thus come to resemble each other, the proportionate advantage was chiefly on the side of the one which was smaller in numbers, and that when the numerical difference was great the advantage to the other could be neglected. The amended law which is quoted above shows, however, that the proportionate advantage is always the same, and this is also enforced in another part of the same letter:—"It must be remembered, however, that B does no harm to A by mimicking it; on the contrary the act of mimicry is of advantage to A over its former state of existence as well as to B; but A being more numerous the advantage is less. Still, after the assimilation, neither has an advantage *over the other*. Proportionally they suffer from the ravages of birds equally; the percentage of losses is the same; they are on equal terms. No matter how long they continue the association, neither gains or loses on the other; though through one being more numerous it loses more individuals, yet equally in proportion with the other. So that if one is twice as numerous as the other at the time of assimilation, it must always—other conditions being equal—remain twice as numerous."

Dr. Müller's interpretation was at first criticized in many quarters, the chief objection brought forward being the belief that birds do not learn the meaning of the conspicuous colours by experience, but that they avoid such insects by instinct, the ancestral experience having become hereditary. There is, however, no direct evidence for this view, and I think the account of J. Jenner Weir's observations upon Lizards, and my own upon Lizards and Frogs (given in the two Appendices to this paper), will go far to furnish an experimental refutation of such a theory, so far as these animals are concerned. In addition to this, I am assured by a very keen observer, Rev. G. J. Burch, that recently hatched chickens certainly do peck at insects which they afterwards learn to avoid without trial, and he believes that the hen assists in their education by indicating that certain insects are not fit for food. His observations were chiefly made upon a common phytophagous Hymenopterous larva which is found upon gooseberry (doubtless *Nematus ribesii*). Another observation made by Mr. Burch bears upon the same question. He offered his chickens a quantity of chickweed, knowing that this plant was often given as food to Linnets. The chickens ate the plant readily enough, but they were all extremely unwell in consequence, and vomited freely. After this Mr. Burch again offered them chickweed, but they had profited by the experience and would not touch it.

The chief attack upon Dr. Müller's suggestion was made by Mr. W.

L. Distant (' Nature,' vol. xxvi. p. 105 ; and ' Rhopalocera Malayana,' pt. ii. p. 33) ; but all his objections were very completely answered by Prof. Meldola (' Ann. & Mag. Nat. Hist.' Dec. 1882), who, in his concluding sentences, largely anticipates that further extension of Fritz Müller's theory which is here brought forward, the suggestion that all the conspicuous and dangerous or distasteful species in any country will be found to share between them a few strongly contrasted colours, arranged in few and simple patterns again and again repeated. He says:—"I am persuaded that the extension of the theory of mimicry proposed by Fritz Müller marks a great advance in our views on this subject, which is so interesting as having been the first to which the Darwinian Theory of Evolution was applied with such success by Mr. Bates. Not only are we now in possession of a consistent theory which enables us to dispense with mysterious and 'unknown local causes,' but other groups of facts hitherto incomprehensible are capable of explanation. Thus the prevalence of one type of marking and colouring throughout immense numbers of species in protected groups, such as the tawny species of *Danais*, the barred *Heliconias*, the blue-black *Euplœas*, and the fulvous *Acræas*, is perfectly intelligible in the light of the new hypothesis. While the unknown factors of species-transformation have in these cases caused divergence in certain characters, other characters, viz. superficial colouring and marking, have been approximated or prevented from diverging by the action of natural selection, every facility having been afforded for the action of this agency *by virtue of the near blood-relationship of the species concerned.* When discussing the origin of mimicry, Mr. Darwin long ago suggested that it might have commenced at a time when the species were nearly related in marking and colouring." The suggestion here brought forward and depending upon the results which are tabulated below, is a further extension of the same principles, so that certain resemblances between insects belonging to very different groups are accounted for on the supposition that natural selection has not only prevented divergence in nearly related forms which were originally similar, but has in other cases actually determined the convergence of widely separated forms which were originally unlike. This latter explanation of the resemblances was intended by Fritz Müller in his paper on "*Ituna* and *Thyridia*," for he looked upon these genera as widely separated, and their similarity as due to convergence. There appears, however, to be some dispute as to their true affinities. It is obvious that under Prof. Meldola's suggestion we shall expect to find a far greater similarity between the species of a large group of closely allied nauseous insects in any country than between those of other large groups protected in other ways ; while, on the other hand, there is no necessity for the expectation of equal uniformity among the isolated nauseous species or even among those belonging to small nauseous groups. We should rather expect the constant appearance of a few simple but very different patterns, made up of a few strongly contrasted colours ; and this is precisely the arrangement which is proved to obtain by the tabulation of the appearances of all such

species known to be nauseous or dangerous. There must certainly be a tendency towards a further general convergence, but the existing condition of convergence round a few well-marked types of pattern and colouring must be highly beneficial, and there was in this case no initial uniformity due to close affinity, upon which to base a general and uniform system. It was in fact *à priori* far more likely that the convergence of remote species should have been round a few successful types, while the prevention of divergence among closely related species must *ipso facto* have tended to produce concentration round a single type. It will be shown below that Fritz Müller's principle is probably attended by others, which also assist in producing convergence, at any rate in some cases.

Another result of the different origin of the two classes of resemblance alluded to above is that the uniform warning colours of a large group of closely related species are less conspicuous, and in themselves possess less of "warning" characteristics, than those of the smaller groups into which the isolated nauseous species tend to converge; for the former depend largely upon some ornamental type of colour and marking, due to sexual selection, and prevalent before the time when the nauseous attributes arose. Such a type has no doubt been modified in the direction of greater conspicuousness on the uppersides of the wings, while bright colours have appeared on their undersides, and the mode of flight has been changed into one which gives the colours their maximum effect; but still, in spite of these changes, the whole appearance of such large groups presents us with the ancestral sexually selected colours and patterns, which are of great beauty, and are no doubt still of great significance as secondary sexual characters. The success of such a stereotyped ornamental appearance for warning purposes has depended upon the modifications alluded to above, but principally upon the very fact of its prevalence and uniformity. On the other hand the smaller convergent groups of nauseous insects often present us with ideally perfect types of warning patterns and colours—simple, crude, strongly contrasted—everything subordinated to the paramount necessity of becoming conspicuous. For the nauseous attributes arising independently among the scattered species of many genera, or in all the species of small genera, instead of being chiefly concentrated among the members of some one or two dominant groups, it must have become impossible to rely upon the slightly altered ornamental appearance existing at the time when the attributes arose; but it was necessary to appeal strongly to the memory of enemies by the acquisition of some special form of pattern and colour, in which everything is subordinated to the "warning" characteristics. In the one class the pre-existing ornamental appearance was sufficiently well known to serve as a warning; in the other class it was not sufficiently well known.

It is quite clear that the two classes of resemblance which have been just considered must be carefully distinguished from true mimicry, in which the mimicking species is without any unpleasant attribute, but shelters itself under the reputation of the (nearly

always) more abundant species which it resembles. In the former classes of resemblance we have groups of two or more conspicuous forms all possessing unpleasant attributes, which become convergent in external appearance, or which maintain an initial uniformity, and in either case are mutually benefited by the process. In the latter class the resemblance would be a source of danger to the mimicked species if the edibility of the mimicking species were discovered; and the experiments detailed in the present paper show how likely it is that such qualities would be discovered if the latter species became relatively abundant. Nevertheless, *until the discovery was made*, the mimicry would be an advantage to both species, for the reasons already adduced. In the following Table the colours of conspicuous insects are tabulated, *i. e.*, those contained in Tables I. and IV., excluding *S. fuciformis* and the conspicuous larva of *L. pini*, the latter being omitted because I have never seen a specimen, and because the appearance differs greatly in the various figures I have been able to consult (see Table A, pp. 232–235).

I have described the colours of the imagos at rest to correspond with the larvæ and pupæ; in flight the following effects are seen:— Imagos of Wasp, *Bombus*, *Nomada marshamella*, *E. jacobææ*, *A. filipendulæ*, *A. grossulariata*, the two Coccinellidæ, *Telephorus* and *Chrysomela*, would show much the same colours as at rest, although in *E. jacobææ* and *A. filipendulæ* the red would be in larger amount because of the under wings, and in the Coccinellidæ, *Telephorus* and *Chrysomela*, the black would be in far larger amount because of the body. The imagos of *S. menthastri*, *S. lubricipeda*, and *P. auriflua* would hardly show the black spots in flight, but would appear whitish, yellowish, and white respectively.

This comparison is exceedingly interesting if it is remembered that the colours which are repeated again and again are those which are known to produce the greatest effect. Thus the greatest possible contrast is afforded by black and white, and next to this by black (or some very dark colour) and yellow, orange, or red, the brightest colours in the spectrum, which possess a far higher illuminating-power than any of the others. Hence we find that the colours of all the conspicuous insects which have been tested are in all except five cases included in the short list given above. And these five only differ in the inclusion of blue in one case, and of green in the other four cases. Hence we probably see that in addition to the advantage gained by convergence which has been alluded to above, benefits have been derived from the colours which have been employed; and as the choice of the most conspicuous colours is limited, it is seen that a certain amount of similarity must follow incidentally from the number of forms of life among which the few combinations are divided. Hence convergence has been aided and perhaps given its starting-point by the action of another principle of coloration also favoured by natural selection, and leading in the same direction as convergence itself (see Table B, pp. 236, 237).

Just as similarity in colours was favoured by the limited number of suitable combinations, so there are a few eminently conspicuous

TABLE A.—*The Colours*

Various classes of Colours. (When incompletely described in this column, the correct details are given in the columns to the right.)	Dark Ground-colour and Lighter Secondary Colours.				
	Species.	Ground-colour.	Colour next in importance.	3rd colour.	4th colour.
I. Black and white or white and black. 2 forms.	Larva of *V. io*	Intense black.	White points.		
II. White, black, and yellow. 3 forms.	.....	.....	.....	.....	.....
III. Black and yellow or yellow and black. 10 forms.	Pupa of *A. grossulariata.*	Black.	Yellow.		
	Imago of *Nomada marshamella.*	Black.	Yellow.		
	Imago of *Vespa vulgaris.*	Black.	Yellow.		
	Imago of many species of *Bombus.*	Dark brown or black.	Yellow or orange.		
	Larva of *V. urticæ*	Black.	Yellow points and often bands.		
	Larva of *P. brassicæ*	Bluish green, with black spots, so that effect is very dark.	Yellow.		
IV. Black and red or red and black. 6 forms.	Imago of *E. jacobææ* (as seen at rest).	Very dark brown; effect black.	Red.		
	Imago of *A. filipendulæ* (as seen at rest).	Greenish black; effect black.	Red.		
	Imago of common species of *Telephorus.*	Black.	Red.		
V. Black, red, and white. 4 forms.	Larva of *D. euphorbiæ.*	Black.	Red.	Yellow or white.	
	Larva of *P. auriflua.*	Black.	Red.	White.	
	Larva of *E. lanestris.*	Black.	Reddish.	White.	
	Larva of *O. antiqua*	Dark brown; effect black.	Pink.	White or yellow.	

of Conspicuous Insects.

Light Ground-colour and Darker Secondary Colours.

Species.	Ground-colour.	Colour next in importance.	3rd colour.	4th colour.
Imago of *S. menthastri* (as seen at rest).	Creamy white.	Black.		
Imago of *A. grossulariata* (as seen at rest).	White.	Black.	Yellow.	
Imago of *P. auriflua* (as seen at rest).	White.	Yellow.	Black.	
Larva of *A. grossulariata* ...	Cream.	Black.	Orange.	
Imago of *S. lubricipeda* (as seen at rest).	Buff.	Black.		
Larva of *E. jacobææ*	Yellow.	Black.		
Larva of *A. filipendulæ* ...	Yellow.	Black.		
Larva of *P. bucephala*	Yellow (becoming orange in parts).	Black.		
Imago of *Coccinella septempunctata*.	Red.	Black.		
Imago of *Coccinella bipunctata*.	Red.	Black.		
Imago of *Chrysomela populi*	Red.	Blue-black.		

TABLE A

Various classes of Colours. (When incompletely described in this column, the correct details are given in the columns to the right).	Dark Ground-colour and Lighter Secondary Colours.				
	Species.	Ground-colour.	Colour next in importance.	3rd colour.	4th colour.
VI. Black, red, blue, and white. 1 form.	Larva of *C. neustria*.	Difficult to determine upon, but probably black, because it occurs so frequently between the other colours and mixed with them; also underside is dark.	Orange-red.	Blue.	White.
VII. Brown, yellow, and black. 1 form.	Larva of *H. defoliaria*.	Reddish brown.	Yellow.	Black.	
VIII. Green, yellow, and black, or green, black, and yellow. 4 forms.	.....	.....	.....	.....	.....

and simple patterns which are in this case especially adapted for the respective stages of the various nauseous or dangerous insects.

Ring-patterns.—Especially suited to the cylindrical body-form, such as that of larvæ, pupæ, or of imagos with colourless wings (Hymenoptera &c.). Accordingly we find this pattern developed in such stages, and it is also often suggested on the visible part of the body of other forms.

Longitudinal Stripes.—Also especially suited to the cylindrical body-form, and accordingly it is entirely found in larvæ and in the attenuated imagos of the genus *Telephorus*.

Spots.—Especially suited to a wide coloured expanse, such as that provided by the wings of Lepidoptera or the elytra of many Coleoptera, but also fairly adapted to the cylindrical body-form, and accordingly it is characteristic of conspicuous Lepidopterous and Coleopterous imagos, only two of the four included larvæ possessing

(*continued*).

Light Ground-colour and Darker Secondary Colours.

Species.	Ground-colour.	Colour next in importance.	3rd colour.	4th colour.
Larva of *C. verbasci*	Pale green.	Yellow.	Black.	
Larva of *D. cæruleocephala*	Smoky green.	Yellow.	Black.	
Larva of *H. wavaria*	Green, varying to lead-colour.	Yellow.	Smoky.	
Larva of *D. galii*	Yellow, varying through light green, olive-green, various shades of brown to black (in the last case should be in opposite column).	Black.	Yellow or white.	

it in at all a marked degree (*A. grossulariata* and *A. filipendulæ*), and one of these is partially striped.

Combination of Ring and Stripe, and of Ring and Spot, and Stripe and Spot.—Also suited to the cylindrical body-form, and occurring in larvæ and in one imago only (*E. jacobææ*).

Hence the existing arrangement of many widely separated conspicuous insects possessing a similar type of pattern is due to the fact that there is a limited choice of available patterns, as well as to the factors conducing to convergence. In addition to this there is probably in some cases a certain amount of true mimicry in the acquisition of patterns and colours. Thus it is more than probable (as has been previously suggested by other observers) that the species rendered conspicuous by alternate rings of black and yellow gain great advantages from the justly respected appearance of Hornets and Wasps. It must not be forgotten, however, that the latter

TABLE B.—*The Patterns of Conspicuous Insects.*

I. RING PATTERNS.

Pattern developed on abdominal segments	Pupa of *A. grossulariata* ...	Alternating rings of yellow and black.
	Imago of *Vespa*, *Nomada*, and *Bombus*.	
Developed on whole length of body.	Larva of *E. jacobææ*	

II. LONGITUDINAL STRIPES.

Stripes numerous	Larva of *P. bucephala*	Alternating stripes of black (or dark ground-colour) and yellow.
Stripes few.....	Larva of *V. urticæ* (a common var.).	
	Larva of *P. brassicæ*	
Stripes few.....	Larva of *D. cæruleocephala*	Smoky green and yellow stripes; black dots. Perhaps should be included in VI.
Stripes few.....	Imago of *Telephorus*.....	Black, with a red stripe on each side.
Smoky stripes many; yellow, one on each side.	Larva of *H. wavaria*	Green (variable), with smoky and yellow stripes.
Striped appearance only visible from the side.	Larva of *H. defoliaria*	Brown above and yellow below; narrow black between.
The one white stripe on each side is due to white hairs; four red stripes.	Larva of *P. auriflua*.....	Black, with red and white stripes.
Single dorsal white; one blue, three orange-red on each side, and black alternating with these in nearly all cases.	Larva of *C. neustria*	Stripes black, orange-red, blue and white.

III. SPOTS.

		Ground.	Spots.
Yellow band and blotch on each fore wing; spots numerous; body yellow, with black spots.	Imago of *A. grossulariata* (as seen at rest).	White.	Black.
Spots numerous.....	Imago of *S. menthastri* (as seen at rest).	White.	Black.
Few black patches and a yellow tuft on end of body.	Imago of *P. auriflua*.....	White.	Black.
Orange stripe; spots few, but far the more important feature; otherwise the larva should be included in VI.	Larva of *A. grossulariata*...	Cream.	Black.
Some of the spots fuse into an irregular line on each fore wing; spots not numerous.	Imago of *S. lubricipeda* (as seen at rest).	Buff.	Black.

TABLE B (*continued*).

		Ground.	Spots.
III. SPOTS (*continued*).			
Spots few	Larva of *A. filipendulæ*	Yellow.	Black.
Seven black spots	Imago of *Coccinella septempunctata.*	Red.	Black.
Two black spots	Imago of *Coccinella bipunctata.*	Red.	Black.
Spots so minute as to produce little effect.	Larva of *V. io*	Black.	White.
Spots so minute as to produce little effect.	Larva of *V. urticæ* (normal form).	Black.	Yellow.
Six spots	Imago of *A. filipendulæ* (as seen at rest).	Black.	Red.
IV. COMBINATION OF RING AND STRIPE.			
Few small white spots also present; rings due to hair-bearing tubercles.	Larva of *E. lanestris*	Black, with incomplete reddish rings and narrow white stripe on each side.	
V. COMBINATION OF RING AND SPOT.			
Spots on the yellow rings...	Larva of *C. verbasci*	Green, with incomplete yellow rings and black spots.	
VI. COMBINATION OF STRIPE AND SPOT.			
Dots very minute and produce little effect.	Larva of *D. euphorbiæ*	Black, with red blotches and stripes and white or yellow dots.	
Two spots and two stripes on each fore wing.	Imago of *E. jacobææ* (as seen at rest).	Black, with red stripes and spots.	
VII. NOT REFERABLE TO THE ABOVE TYPES.			
One blotch on each segment. Perhaps referable to the spot-pattern III.	Larva of *D. galii*	Variable ground-colour, with a row of black blotches, each containing a pale area.	
The pink colour is scattered in a kind of spot and stripe system.	Larva of *O. antiqua*	The effect chiefly made up by the dark- and light-coloured tufts of hair.	
Two unequal areas with opposite colours.	Imago of *Chrysomela populi*	Large posterior part red, small anterior part blue-black.	

The patterns in flight in the imagos would be different in many cases. In *E. jacobææ* and *A. filipendulæ* a conspicuous but confused mixture of red and black is seen. The slow flight of *A. grossulariata* permits its pattern to be seen almost as at rest. The others are as above described after Table A.

forms also probably gain to some extent by the greater publicity which follows from the resemblance. We therefore see that the force which tends towards the acquisition of similar forms of colour and marking in widely different organisms is itself the resultant of other forces varying in relative amounts in the different species. Of these primary forces we have been enabled to detect two in the majority of cases, and three in the minority, *i. e.* (1) The feasibility of certain colours and patterns depending upon their effect on the vertebrate eye, and thus giving the enemies as easy an education as possible; (2) The advantage of facilitating the education of enemies by giving them a small number of patterns and colours to learn; and (3) The great additional advantage conferred by trading upon the reputation of a well-known and much-feared or much-disliked insect.

These may probably be looked upon as the chief primary forces which have determined the various forms of conspicuous appearance. But such forces have had very different material to work upon in the different species, and doubtless the resultant has been largely influenced by the protective colours which existed before the "warning" colours and markings arose, and which formed the material on which the first steps (at any rate) were built. We can, in fact, point to certain conditions in the "warning" appearance of some species which are almost certainly remnants of a previous mode of defence due to protective coloration. Thus Prof. Meldola has drawn my attention to an opinion expressed by Mr. T. W. Wood ("Insects in Disguise," Student, 1868), that the larvæ of *E. jacobææ* are protected by their resemblance to the flowers of the ragwort. I believe that in the orange ground-colour of this species we have such a remnant of a former resemblance to the flowers of this plant and the groundsel, on which the species also feeds. The acquisition of the black bands and, above all, the gregarious habits are, then, later developments which have followed the acquisition of an unpleasant taste. Here it is seen that the material at the disposal of the primary forces tending towards a "warning" appearance was such as to render most probable the resultant which has actually obtained.

Again, Mr. Thomas Eedle informed Prof. Meldola that he believed the larva of *C. verbasci* resembles the flowers of its food-plant, mullein. Here, again, I entirely agree with this observation. There is a great deal in the larva which harmonizes extremely well with the yellow and dark sessile flowers, studded upon the surface of the thick green spike, and surrounded by green unopened flowers. In this case it is probable that the pattern may have been rendered a little more distinct; but the very conspicuous appearance practically depends upon the gregarious habit, and upon the fact that the larvæ do not chiefly rest upon the spike, but are commonly seen upon the uppersides of the large leaves, forming a background against which the larval colours appear with startling distinctness. But, as Mr. Eedle maintains, an isolated larva on the flowering-spike is evidently well protected by colour-harmony with its surroundings. These are but instances of the past history which must be deciphered before we

can adequately appreciate the meaning of the colours and markings of any animal.

III. *Insects which evade their Enemies.*

We now come to Wallace's converse suggestion—that just as conspicuous forms which court observation will be avoided, so the insects which harmonize with their surroundings, and which evade their enemies, will be greedily eaten when detected and caught. I have adopted Meldola's suggestion that the terms "protective resemblance" should be applied to the appearances which tend to deceive enemies by their resemblance to motionless (vegetal or mineral) surroundings, the term "mimicry" denoting the resemblance to other animals. On entering upon the experimental investigation, I thought that I should have little to record except a complete agreement with everything which has been previously said upon the subject. I was surprised, however, to find some instances which are entirely antagonistic to the principles laid down by Wallace. Unfortunately the instances recorded by other observers are exceedingly few. Jenner Weir evidently experimented with a large number of species, but he gives very few details, and for the most part is content with summing-up his results as favourable, without exception, to Wallace's suggestion, in these words:—"I will now add a few words on those larvæ which are eaten greedily by birds, and my remarks on the subject will be brief; it will be unnecessary to detail all the experiments made, as the results are easily generalized.

"All caterpillars whose habits are nocturnal, dull-coloured, with fleshy bodies and smooth skins, are eaten with the greatest avidity.

"Every species of green caterpillar is also much relished.

"All Geometræ, whose larvæ resemble twigs as they stand out from the plant on their anal prolegs, are invariably eaten. . . . . They eat with great relish all smooth-skinned larvæ of a green or dull-brown colour, which are nearly always nocturnal in their habits, or mimic the colour or appearance of the plant they frequent."

Jenner Weir, however, gives details of experiments with other stages of Lepidoptera; and I am now able to add many valuable details from his experiments upon Lizards in 1886. There are also a few instances to include from Mr. Butler's paper (already quoted) and a few of which I have heard from him by letter. In my experiments I chiefly made use of the imagos of Lepidoptera, as I nearly always sought for conspicuous larvæ with which to test the suggestion previously discussed.

Other observers having given so little detail, it follows that Wallace's converse suggestion possesses extremely little precisely recorded experimental foundation. There is, however, no reason to doubt that Jenner Weir's conclusions will be very generally confirmed by extended experiments, and they doubtless express the results of many observations. But as I have come across a few startling exceptions among the most protectively coloured forms, it is safer not

to assume the existence of any great body of confirmatory evidence until it has all been rigidly tested and recorded.

It will be unnecessary to separate the larvæ from the other stages, because the meaning of imitative colours is equally clear whenever they occur, while the warning colours of imagos might in some cases be mistaken for those of other significance. I will proceed at once to tabulate everything I have been able to find recorded, and will afterwards consider in detail the more remarkable cases. I have already implied that I believe the larvæ of *Papilio machaon* should be included in the Table given below. Prof. Meldola has since shown me that Mr. T. W. Wood has also taken this view of the colours of *P. machaon* (see a paper in 'The Student,' 1868, entitled "Insects in Disguise"). I believe that the bright green colouring broken up by black markings is very well adapted for concealment among the much-divided leaves of the Umbelliferæ on which the larva feeds. I also consider that the imago of *S. fuciformis* should be included (see Table V., pp. 242–259).

Looking back at this list we see that as a whole its results offer the most decided contrast to those of the previous lists, inasmuch as the vast majority of species are in this case devoured with relish. But while it thus supports the converse side of Wallace's suggestion, this is by no means so universally true as Jenner Weir's earlier experiments led him to believe. Out of a total of 44 different species, or stages, of Lepidoptera, we find 7 exceptions, viz:—Imagos of *S. ligustri*, *P. bucephala*, and *O. antiqua*; pupæ of *V. io*, *V. urticæ*, *P. bucephala*; and the larva of *M. typica*. Two of these appear for the first time in Table V., while the others have appeared before in other stages in the earlier tables. Deferring the consideration of the latter, we will take the two species rather more in detail.

Imago of Sphinx ligustri.—I think the evidence in this case speaks for itself, and demonstrates very completely the protective importance of mere size, unaccompanied by other alarming features or by any means of active defence. The species is admirably protected at rest and must be most carefully concealed. After twenty years, during which I have looked for insects, I have only once seen the moth at rest. Again, its flight is probably as rapid as that of any species in the world. The behaviour of *Lacerta viridis* seemed to clearly show that the moth was highly palatable, as we should expect from its very perfect means of evading its enemies. And yet the much smaller *L. muralis* would not touch the insect. If the supposition be raised that the moth possessed some smell, which was disliked by *L. muralis*, but to which *L. viridis* was indifferent, I can only say that I have met with no other instance of any difference of tastes when I experimented upon the two Lizards with the same species of insect. And if this be the correct explanation why the moth was untouched after spending many hours in the cage of *L. muralis*, I cannot but think that *L. viridis* would have shown some reluctance in devouring it, although it might have ultimately eaten it under the impulse of hunger. And, again, *L. muralis* was more ravenous than any of my Lizards; and the above tables show clearly that I have

chiefly relied upon this species for the evidence that hunger will force a Vertebrate to eat an insect which is evidently distasteful to it. Further the *L. viridis* being less used for this purpose, were not pressed by hunger to the same extent as *L. muralis*. I think that the almost certain explanation is that *L. muralis* was afraid to touch an insect which was not far from its own size, while *L. viridis* was less timid, the difference in size being far greater. And such an explanation throws light on the cases already discussed, in which a large caterpillar is protected by gaining some marking which suggests the appearance of a serpent. On this point Weismann says (Meldola's translation as above, p. 330):—"It does not require much imagination to see in such a caterpillar an alarming monster with fiery eyes, *especially if we consider the size which it must appear to an enemy such as a lizard or small bird.*" The case of *S. ligustri* enforces this last remark, and shows how size *alone* may be efficient as a protection against the smaller insect-eating Vertebrates. So far as I am aware, this important use of size, unaccompanied by any accessory markings or any special attitude, is now brought forward for the first time; but it is an advantage which is probably far from uncommon, considering the number of large species in the same position as *S. ligustri*, and it has doubtless been of special importance as an initial stage in the development of the more elaborated forms of terrifying appearance already described.

Larva of Mania typica.—In this case it was perfectly clear that the larva possessed a very unpleasant taste, so that it was refused by *L. muralis* even when very hungry. And yet the description given in the table shows that the species is highly protected in the larval state by protective colouring and habits which correspond. As the exception is so important, I will add a few details to the proofs given in the table. Newman gives the following facts about the young larvæ: when hatched from the eggs laid upon the leaves of pear, plum, &c., the larvæ "devour the upper cuticle and parenchyma of the leaf, leaving the lower cuticle entire, dry and brown; they lie closely packed side by side and apparently motionless," but in reality gradually moving onwards, "leaving a larger brown space behind." We see here a most interesting adaptation of the surroundings to the brown colour of the larva. A brown larva is conspicuous on a green leaf, and a single larva could not eat away the cuticle so as to surround itself with a brown area of sufficient size until after the lapse of considerable time. Hence the subordination of gregarious habits to ends which are the exact opposite of those usually sought, viz. the intensification of warning colours. We have therefore a most elaborate and perfect mode of concealment in the younger stages of larval life. It is obvious, however, that such a method can only be successfully adopted while the larvæ are very small, so that a large number of them can rest for a long time on a single leaf. Accordingly Newman tells us that "in a few days, perhaps from ten to fifteen, they abandon this arboreal life," and descending, feed upon many kinds of low-growing plants. It hybernates in October, and again feeds greedily in the following spring; but,

TABLE V.—*Experiments with Insects which are protectively*

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	1. LEPIDOPTEROUS
Larva *Saturnia carpini* ...	The green larva with its black bands and pink tubercles harmonizes remarkably well with the heather on which it feeds (*Andrew Murray*: quoted by Wallace in the essay often referred to). The larva feeds on other plants also, but the special relation of its appearance to that of heather seems to indicate that this is its ancestral food-plant. Very often, however, the larva possesses golden instead of pink tubercles.
Larva *Mamestra brassicæ*...	Commonest variety is olive-brown dorsally and dingy yellow ventrally, with abrupt line of demarcation; a triangular mark containing two white dots on the back of each segment. Other varieties are brown or dingy green or any intermediate tint. Well concealed among the leaves or in tunnels, in cabbage, broccoli, &c., but freely exposed on many plants, although always harmonizing with the surroundings.
Larva *Tryphæna orbona*...	Colour dingy umber-brown, with darker and paler markings. Feeds on low plants, and in spring on sallow and hawthorn.
Larva *Tryphæna pronuba*..	Larva concealed by day, feeding at night on almost all the plants in gardens. Colour varies from pale yellowish green to dark brown, with brown, black, and pale markings.
Larva *Tæniocampa gothica*	The whole effect of the larva is green (green ground-colour with one lateral white stripe, and a dorsal and two lateral very narrow pale yellow stripes). Hence harmonizes well with the leaves of the many plants on which it feeds. Disturbed it falls off and has some chance of escaping in the grass or other low-growing plants.
Larva *Phlogophora meticulosa*.	The whole effect green or brown (for the larva is dimorphic), as the white dorsal and lateral stripes are inconspicuous. Hence well protected on leaves of food-plant, and the brown varieties on dead leaves and earth. Same protective habit of falling off as noticed in *T. gothica*. Feeds on many low-growing plants.
Larva *Mania typica*	The larva is coloured with various shades of brown, and is most perfectly protected against brown leaves, which, as I have observed, it almost invariably selects, and upon which it sits motionless by day, feeding at night. If there are no brown leaves it retires by day into a very dark corner among the green leaves. It also has the habit of falling off. Feeds on many trees and low-growing plants.
Larva *Hyponomeuta euonymellus*.	Yellowish grey with black spots, not conspicuous in themselves; but the larvæ live in colonies, spinning a web, the latter certainly attracting attention. But the larvæ seem to be safe within it, as in a cocoon. The gregarious nature is doubtless related to the habit of spinning a common web. Feeds on spindle.

Coloured, or which evade their Enemies by other means.

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
LARVÆ.	.....	A. Weismann.—Devoured by *Lacerta viridis*.	Support.
.....	.....	A. G. Butler.—Eaten by *L. viridis*. Larvæ of this genus and of *Hadena* eaten by many birds (*e. g.*, Robins).	Support.
.....	Eaten by Lizards ...	.....	Support, as with last species.
.....	Eaten by *Zootoca vivipara*.	.....	Strong support, from the special character of the concealment.
Eaten greedily by *L. muralis*. The larvæ had been found on *Aconitum napellus*, but the Lizards were unharmed by the poisonous food in the larval digestive canal.	.....	.....	Support.
Eaten greedily by *Hyla*	.....	.....	Support.
At once attacked by *L. muralis*, the larva being immediately detected, although rolled up and motionless. Nevertheless the Lizard evidently much disliked it, and after being severely bitten, it was rejected; others tasted the larva with the same result.	.....	.....	At first sight a most startling difficulty. Yet it was evident, from the behaviour of the Lizards, that they fully expected the larva to be palatable; in itself a strong confirmation of the suggestion that nearly all such larvæ are palatable.
.....	The "larvæ only which ventured beyond the protection of the web were eaten" by birds. The birds "appear very much to dislike the web sticking to their beaks."	.....	Support. Being defended by the web there is no necessity for a specially perfect form of protective resemblance.

TABLE V.

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	2. LEPIDOPTEROUS
Pupa *Vanessa io*	Dimorphic: a dark grey variety with a small amount of gold, and a yellowish-green variety with a larger amount. Some have thought that the gold is a "warning" colour, but I have shown that the green form can be produced to the exclusion of the other by placing the larva in green surroundings before pupation (see Proc. Roy. Soc. vol. xlii. p. 95). W. H. Harwood also informs me that the green form is often found on the leaves of nettles, while the other is the ordinary form, on stones, walls, &c. Hence we have in this pupa the very highest kind of protective resemblance, *i. e.* one that is adjustable to the differences between the various surroundings to which the organism is likely to be exposed.
Pupa *Vanessa urticæ*	Varying from very dark grey (almost black), with hardly any gold, to very light pinkish varieties, with much gold, and in some cases the pupæ are gilt all over. No green form. As above, the gilded appearance can be controlled by placing the larva in gilt surroundings (see Proc. Roy. Soc. vol. xlii. p. 95); while the dark forms may be produced by using black surroundings.
Pupa *Pygæra bucephala* ...	Dark reddish brown, and well protected upon or in the earth and under dead leaves &c., these being invariably the places chosen by the larva for pupation.
Pupa *Mamestra brassicæ* (almost certainly this species).	Light reddish brown: protected by being buried some slight depth in the earth. If accidentally exposed, it harmonizes fairly well with the earth.
Pupa *Tryphæna pronuba* (almost certainly this species).	Reddish brown, and protected as in the last species .....
Pupa *Plusia gamma*.....	A black chrysalis protected in a cocoon .....
	3. LEPIDOPTEROUS
Imago *Pieris brassicæ*	Protected by strong flight, and by its yellowish and black undersides harmonizing well with the yellow or white flowers of Cruciferæ, which it chiefly frequents. It is also very effectually concealed during prolonged rest (night, or during rain), for it is not commonly seen at rest, except in the intervals of flight, although such a very abundant Butterfly.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
PUPÆ.			
.....	Refused by the birds	.....	A difficulty: in view of the extremely complete form of protective resemblance. It would be interesting to experiment with other Vertebrates and with hungry birds.
Freely eaten by *L. muralis*	Refused by the birds	.....	Same difficulty with birds ; the same high form of protection. In this case, however, the Lizards freely ate the pupæ, and they are evidently palatable to these Vertebrates.
Bitten by *L. muralis*, but evidently much disliked and abandoned: some were eventually partially eaten when the Lizards were very hungry.	.....	Edward Newman in 'British Moths.' — "They also constitute a favourite food of poultry, and are sought for with great eagerness."	Concerning the behaviour of the Lizards, it is to be noted that the pupal colour is not a very specialized form of protection, although complete, for it equally obtains in species which pupate in opaque cocoons &c.
Eaten with great relish by *L. muralis*, slightly crushed, and then swallowed whole. Great contrast to the treatment of the last species.	.....	Edward Newman in 'British Moths.'—Fowls, Guinea-fowls, Pea-fowls, and Pheasants devour them with the greatest avidity.	Support.
Eaten at once and evidently relished by *L. muralis*.	.....	.....	Support.
Eaten at once (removed from the cocoon) by *L. muralis*, and probably relished.	.....	.....	Support.
IMAGINES.			
Eaten readily by all Lizards, but not much relished, I believe, because of the mechanical difficulty of the scales and wings, and not from being actually unpalatable. This applies to all Butterflies, and Moths to a less extent.	Eaten by Lizards ...	Roland Trimen.—A Swallow seen chasing this species (Trans. Linn. Soc. vol. xxvi. p. 499, footnote). A.G.Butler.—Eaten by *L. viridis*.	Support.

TABLE V.

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	3. LEPIDOPTEROUS
Imago *Pieris rapæ*	Same as the last species, but not such strong flight; on the other hand, its smaller size renders its concealment more perfect.
Imago *Pieris napi*	Flight rather weaker than in the last species. Protection otherwise similar, except that the green veining of the undersides accords well with the fact that the species especially prefers shady places, where green is the predominant colour.
Imago *Anthocharis cardamines.*	Flight irregular and puzzling, although not rapid. The green and white mottled under surface of the wings harmonizes exceedingly well with the green and white flower-heads of Umbelliferæ, which are especially selected as a resting-place (T. W. Wood, quoted by Wallace). The orange patch on the male's fore wing is not conspicuous on the underside.
Imago *Vanessa io*	Flight strong: underside very dark and the insect well concealed on dark trunks, earth, or in shaded corners. Insect seldom seen at rest, except in intervals of flight, hence well concealed at night &c.
Imago *Vanessa urticæ*.....	As in the last species, only smaller and so more readily concealed: undersides not so dark and more variegated, but well concealed in the same places.
Imago *Smerinthus populi* ..	Flight feeble: in the evening. The irregular outline of the wings, the way they are held, their grey and brown tints (which are alone seen in repose), all render the insect highly protected by suggesting withered leaves. They are also generally well concealed in dark corners, for they are not commonly seen at rest.
Imago *Sphinx ligustri*.....	Flight extremely powerful: in the evening. The various shades of brown of the fore wings and thorax are alone seen at rest, and the insect suggests bark, or even more closely the wood of a cleft tree darkened with age. It is very rarely seen at rest, although an abundant species.
Imago *Hepialus lupulinus*..	Flight very peculiar and puzzling, consisting of rapid oscillations, always taking place near the ground, and for a short time at dusk and in the early morning. At other times, when resting, very difficult to see, because of its small size and attitude, which exposes the brown tints of upper wings, with white markings, and of the body. It thus harmonizes with any of the brown surroundings (earth or dead leaves &c.), and is seldom detected, although exceedingly abundant. When disturbed it feigns death and falls to the ground, where it is very difficult to find.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
IMAGINES (*continued*).			
As in the last species	Eaten by Lizards ...	T. G. B., in 'Nature' (vol. iii. p. 166), has often seen Sparrows capture the species. A. G. Butler has seen the same (information to Prof. Meldola). A. G. Butler.—Eaten by *L. viridis*.	Support.
As above. Also eaten readily by *Hyla*.	.....	.....	Support.
As above. Also eaten readily by *Hyla*.	.....	.....	Support.
Eaten readily by the Lizards, but not much relished, as above.	.....	.....	Support.
As above. Also eaten readily by some of the *Hylæ*, but refused by others.	Refused by all the Lizards.	.....	Support. I have no doubt that the refusal of some Frogs was due to scales only. Jenner Weir's Lizards were probably not hungry.
Eaten by *L. viridis* and *L. muralis*. I think more relished than the Butterflies.	.....	.....	Support.
Untouched by *L. muralis*, but eaten at once by *L. viridis*. Experiment repeated later with same result.	.....	.....	Support from behaviour of *L. viridis*; that of *L. muralis* is exceedingly interesting, and probably introduces a new mode of protection by intimidation resulting from mere size, with no other terrifying quality.
Eaten readily by *L. muralis* ...	.....	.....	Support.

TABLE V.

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	3. LEPIDOPTEROUS
Imago *Cerura vinula*	Flight not powerful: in the evening. At rest the fore wings and body are seen, and are grey with darker markings. The insect is large and apparently not inconspicuous; but it must be carefully concealed, for it is not commonly found, although so abundant a species.
Imago *Pygæra bucephala* ..	Flight not powerful: in the evening. At rest it is "like the broken end of a lichen-covered branch" (*Wallace*, as above). This effect is produced by the purple and pearly-grey colour of the fore wings, with brown markings, and the ochreous tip, and by the ochreous head and thorax. A very perfect form of imitative resemblance, the wings being rolled round the body so as to produce a cylindrical shape, with yellow ends, like a broken piece of decayed stick.
Imago *Dasychira pudibunda*	Flight not powerful: in the evening. At rest the colours, due to fore wings and body, are grey with darker markings. Although common, it is rarely seen, and must be carefully concealed.
Imago *Orgyia antiqua* (female).	The female Moth has rudimentary wings, and never quits its cocoon, but sits on the outside of it, being very inconspicuous, as it is covered with grey down, which harmonizes well with the colour of the surface upon which it is resting.
Imago *Acronycta psi*.....	Flight rapid: at night. Rests by day "on the north side of trees," and therefore protected by resembling lichens (*Wallace*, as above). Fore wings and body alone seen at rest—grey, with dark markings. I have certainly often seen it on other aspects than north; but anywhere on rough bark it is well concealed.
Imago *Mamestra brassicæ* ..	Flight rapid: at night. By day well concealed by the tints of fore wings and part of body, which are "dark smoky grey-brown, with confused markings both darker and paler" (*Newman*); thus well protected on trunks, rocks, &c.
Imago *Mamestra persicariæ*	Flight rapid: at night. By day well concealed (probably in dark corners), as it is seldom seen at rest. The fore wings and part of body alone seen, and are "rich dark bistre-brown" (*Newman*), with a white spot with a darker nucleus in the centre of the wing.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
IMAGINES (*continued*).			
Eaten at once by *L. viridis*.....	.....	.....	Support.
Often refused by all the Lizards, with every sign of disgust, but they were induced to eat them by hunger, and seemed to get somewhat accustomed to the diet. Large numbers employed in the experiments.	.....	.....	A very remarkable exception, when we consider the extremely perfect protective resemblance, which is so highly elaborated in all its details.
Eaten at once by *Hyla*, after other individuals had refused it. Offered to *L. muralis*; it was seized and eaten directly it was seen to move.	.....	.....	Support.
.....	"The only Lepidopterous insect entirely rejected in the perfect state." Disregarded by all the birds except Robin and Reed-Bunting, and refused by these after examination.	.....	Another difficulty.
At once taken and evidently much relished by *L. muralis*. Also eaten at once by some Frogs after refusal by others (experiment repeated).	.....	.....	Support.
Eaten by *L. muralis*.....	Eaten by Lizards ...	.....	Support.
Eaten at once by *L. muralis*, and evidently much relished, as it was seized and swallowed immediately.	.....	....	Support.

TABLE V.

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	3. LEPIDOPTEROUS
Imago *Tryphæna fimbria* ..	Flight rapid: at night. By day very well concealed, probably near the ground and among dead brown leaves. Fore wings and part of body different shades of brown, and also olive-green in other varieties, with paler and darker markings and lines. Hind wings orange, with a broad black border, seen in flight, and with the orange and black on the undersides suggest, in the rapid motion, a yellow leaf blown by the wind. Probably the significance of the markings and the habits are the same as in the next species.
Imago *Tryphæna orbona* ...	Flight rapid: at night; not so easily disturbed by day as *T. pronuba*, but the same rapid flight and habits of concealment &c. if it is disturbed. The colours and protective resemblance are much the same as in the last species.
Imago *Tryphæna pronuba*..	Flight rapid: at night, and also easily disturbed by day, when it flies with great speed, rising very quickly and dropping down (always into good shelter of brown leaves &c.) equally quickly. The whole process is very unlike the flight of a Moth, and the colour and movement suggest a yellow leaf lifted off the ground by a gust of wind, whirled away for a certain distance, and then suddenly falling again; so exact is this resemblance, that I have rarely been certain of the Moth until it had flown a long way. If tracked down and followed the Moth rises again very readily. This resemblance is chiefly due to the brown of the fore wings, aided by the yellow and black of the hind wings and the undersides. At rest it is extremely well concealed by the varying brown shades of the fore wings and part of the body exposed. It seeks dark corners, and hides deeply among thick leaves or among dead leaves on the ground. It is also very strong and slippery, and hard to hold when caught (*Jenner Weir*). I have also noticed this feature. I should add that Jenner Weir has another theory (alluded to below) as to the meaning of yellow and black underwings.
Imago *Anthocelis pistacina*.	Flight rapid: at night; by day well concealed and seldom seen. The parts seen at rest vary much in colour, being brownish, reddish, or of different grey tints with faint darker markings.
Imago *Euplexia lucipara*...	Flight rapid: at night. Very seldom seen at rest, and evidently well concealed, probably in dark corners and among dead leaves. Fore wings and part of body alone seen are rich brown with pale markings and a white mark on the wing.
Imago *Amphipyra pyramidea*.	Flight rapid: at night; by day well concealed and very seldom seen. The parts seen at rest are brown and grey-brown, with paler and darker markings.
Imago *Hadena oleracea* ...	Flight rapid: at night. At rest well concealed and seldom seen. Fore wings and part of body seen are reddish brown, with a narrow white line and two light spots on wings. Resembling bark or dead leaves &c.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
IMAGINES (*continued*).			
.....	J. Jenner Weir has seen a Swallow chase this Moth by day, making "several ineffectual attempts to seize it." The Moth, however, escaped. It was evidently considered a very desirable capture.	.....	Support.
.....	Eaten by Lizards...	.....	Strong support, as in *T. pronuba*. There is no doubt that it is also relished by birds.
I have often seen it pursued by birds with great persistence; they evidently relish it much, and make great efforts to catch it.	Evidently much appreciated by the birds, but even in the aviary its rapid movements and slipperiness made it very difficult to capture. Eaten by Lizards.	.....	Strong support in the special character of the defence suited to so many emergencies; protected at rest; again, when detected or disturbed, by appearance and mode of flight; and, again, when captured, by it slipperiness and great strength; and all this coexisting with and following from the fact that it is keenly relished and much pursued.
.....	Eaten greedily by Lizards, but apparently swallowed with difficulty, probably because of the scales.	.....	Support.
Eaten directly by *L. muralis*, and evidently relished.	.....	.....	Support.
.....	Eaten by Lizards ...	.....	Support.
Eaten by *L. muralis*.....	.....	.....	Support.

TABLE V.

Species and Stage.	Protective resemblance, or habits of concealment, evasion, &c.
	3. LEPIDOPTEROUS
Imago *Cucullia verbasci* ...	Flight (probably) rapid: at night. At rest exceedingly well protected by a most perfect resemblance, both in shape and colour, to a splinter of wood; the colours of the parts seen being rich umber-brown, shading into pale wainscot-brown, and this again into the darker colour.
Imago *Gonoptera libatrix* ..	Flight rather slow: at night. At rest beautifully protected by a most special resemblance to a decayed red leaf with white spots of fungoid growth on it. The parts seen are grey with a reddish tinge, with patches of orange-red and light grey lines, and two minute but intensely white spots on each wing. Similar white marks occur on the legs, which are often partially seen at rest. The effect is greatly heightened by the irregularly toothed margin of the wings. The Moth appears in August and September, and hybernates, so that it is in the perfect state when red and brown leaves are chiefly seen, and when green leaves are mostly absent. It selects dark places in which to hybernate—tool-houses, attics, &c.
Imago *Ennomos angularia.*	Flight slow: in the evening. The angulated wings are yellow with brown lines and short brown streaks, and this colour and shape, together with the attitude and the colour of the undersides of wings (also often seen), all suggest a yellow leaf in a very perfect manner, aided by the time of appearance (August and September).
Imago *Amphidasis betularia.*	Flight slow: in the evening. Both wings and body seen at rest, and dingy white with smoky markings (the latter may suffuse the whole surface in some varieties). Although conspicuous when found at rest, it must generally be concealed with care, for it is not found very commonly at rest, although such an abundant Moth. The protective resemblance may be to variegated lichens on rocks and trees.
Imago *Halia wavaria*	Flight not rapid: in the evening; also easily disturbed by day. Both wings seen at rest (as is usual in Geometræ), and they and the body are grey; the wings with a purplish and brownish tinge, with brown spots and streaks (including the V-like mark). It is thus inconspicuous on tree-trunks &c., although without any special resemblance.
Imago *Camptogramma bilineata.*	Insect conspicuous on the wing. Flight not rapid: in the evening; also very easily disturbed by day. Well concealed in thick leaves when at rest. Wings and body yellow; former with slender white and brown waved lines. A variable amount of brown colouring.
Imago *Chloephora prasinana*	Flight rapid: in the evening. By day beautifully protected by resembling the green colour of foliage; the only parts seen (fore wings and part of body) being yellowish green with three silvery lines across the wing; these latter, on the opposite wings, come together at an angle during the attitude of rest, and convey the impression of leaf-veining. Moth flies in June.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
IMAGINES (*continued*).			
.....	Greedily devoured by the birds.	.....	Support.
Eaten at once by *L. muralis*, and evidently much relished. The Moth was detected while motionless.	.....	F. W. Andrewes informs me that he has seen a Robin carry the Moth off, having flown quite near to him in pursuit of it.	Strong support, because of the special character of protection and the evident keenness with which the Moth is pursued.
Eaten at once by *L. muralis*, and evidently relished. Eaten in large numbers by the *Hyla*; although individuals would refuse them, yet they were generally taken; and sometimes one Frog would take as many as five, one after the other.	.....	.....	Strong support, as in the last species.
Eaten at once by *L. muralis*. Evidently relished.	.....	.....	Support, for it certainly evades its enemies.
.....	Eaten by Lizards ...	A. G. Butler.—Greedily devoured by Frogs.	Support.
.....	Eaten by Lizards ...	.....	Support, for the insect clearly avoids its enemies. But the protection does not seem to be very perfect.
Eaten at once and with apparent relish by *L. muralis*. It was seized directly it was seen to move, not before.	.....	.....	Strong support.

TABLE V.

Species and Class or Order.	Protective resemblance, or habits of concealment, evasion, &c.
	4. IMAGINES OF OTHER INSECTS AND A FEW
CRUSTACEA.	(The arrangement of Claus's 'Text-
Armadillo vulgaris	Dark colour and habits of concealment are strongly protective.
ARACHNIDA.	
Spiders of different species.	*Epeira diadema* and *Tegenaria domestica* were chiefly employed in some of the experiments (E. B. P.), but any common Spiders which could be found were offered to the Lizards and Frogs. In appearance, and especially in their rapid retreat into concealment, the Spiders are difficult to capture, especially when it has been shown that the enemies do not like the web in their mouths.
MYRIAPODA.	
Iulus terrestris	The dark colour and habits of concealment are strongly protective, but it also possesses a very unpleasant odour.
Lithobius forficatus	The brownish orange colour, and especially habits of concealment, are strongly protective: inodorous.
ORTHOPTERA.	
Forficula auricularia	Probably this common species of Earwig was always employed. The colour and habits of concealment are strongly protective. The pincers may perhaps, in some cases, act as "terrifying" structures. The insect has a very disagreeable smell.
Periplaneta orientalis	The colour, rapid movements, and habits of concealment are strongly protective, but the insects also emit a very unpleasant odour.
Decticus verucivorus.....	A large green grasshopper, with brown spots on the fore wings. Thus well concealed, and evidently a very powerful hopper.
NEUROPTERA.	
Chrysopa perla.....	Probably this common species was employed. Its green colour protects the insect among the leaves in which it lives, but it can also emit a peculiarly unpleasant odour.

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
ARTHROPODA OF OTHER CLASSES. book of Zoology' is followed.) Eaten readily by *L. muralis* ...	.....	.....	Strong support.
Always eaten with especial relish by the Lizards and the Frogs.	Spiders eaten greedily by Lizards.	A.G. Butler.—Eaten by *Lacerta viridis*.	Strong support.
.....	.....	A. Weismann.—Refused by *L. viridis*.	A modification: here are unpleasant attributes coexisting with protective habits and colouring.
.....	.....	A. Weismann.—Greedily eaten by *L. viridis*.	Strong support.
Eaten readily by the Frogs.....	Eaten by the Lizards	.....	In this case the enemies made use of did not seem to object to the smell. Support.
Eaten readily in large numbers by all the species of Lizards and by the *Hyla*.	.....	.....	As above; unpleasant attributes coexist with protective habits &c., but the former do not protect them from these enemies.
.....	.....	A. Weismann.—Once eaten by *L. viridis*.	Strong support.
.....	Eaten by *L. viridis*.	.....	Conclusion as in the case of *Periplaneta*. The Lizards are evidently much repelled by certain smells, but do not object to others which are very unpleasant to man.

TABLE V.

Species and Class or Order.	Protective resemblance, or habits of concealment, evasion, &c.
HEMIPTERA.	4. IMAGINES OF OTHER INSECTS AND A FEW ARTHROPODA
Aphis hederæ and Aphides, sp.?	*Aphis hederæ* is dark and inconspicuous; aphides are generally inconspicuous, but probably also, in some cases, protected in other ways (taste or smell).
Hemipteron, sp.?	The species made use of was inconspicuous; but many possess warning-colours. The species was, however, evil-smelling, like the brilliant ones.
DIPTERA.	
Muscidæ of various species	*Musca domestica* and *M. vomitoria* chiefly employed; but also any other Muscidæ which could be found. The appearance, and especially the rapid flight and readiness with which they are disturbed, are strongly protective. Larvæ and pupæ also made use of: both concealed.
Eristalis and *Syrphus*	Probably the commonest species. Although somewhat less well-concealed than many species of *Musca*, many of the species of these genera are even stronger on the wing.
Tipula oleracea.....	Inconspicuous and easily disturbed .....
Bibio marci	The common male is black and inconspicuous: the much less common female orange-coloured and easily seen; both fly readily when disturbed.
COLEOPTERA.	
Melolontha vulgaris	The brown colouring is certainly protective; flight in the evening .....
Carabus hortensis (Fabr.)...	The dark colour and habits of concealment are certainly protective. Nocturnal habits also.
Omaseus melanarius.....	As above, the species being similar in habits and appearance, only much smaller. Nocturnal habits.
HYMENOPTERA.	
Trichiosoma lucorum	Dark colours and flight are evidently protective.....
Cocoons of Ants, sp.?	Carefully protected, being well concealed in the galleries &c. .....

(*continued*).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
OF OTHER CLASSES (*continued*).			
Aphis hederæ freely eaten by young *Hylæ*.	Aphides? sp., eaten by *L. viridis*, *L. agilis*, and *Z. vivipara*. On another occasion hardly noticed by the Lizards.	.....	Conclusion for Aphides? sp.: probably as above: the Lizards evidently dislike the taste, but will eat the insects when hungry. The treatment of *Aphis hederæ* supports conclusions.
.....	Refused by the Lizards after tasting.	.....	The unpleasant qualities evidently a defence in this case.
Eaten greedily and in almost any numbers by Lizards of all the species and by *Hyla*. The latter was especially keen in capturing them, but did not much care for the larvæ, which, with the pupæ, were eaten in large numbers by the Lizards.	Eaten with relish by all the species of Lizards, and in very large numbers. The larvæ and pupæ also eaten.	Eaten by *L. viridis* (*A. G. Butler*).	Strong support.
Keenly relished by the Frogs...	Eaten voraciously by all the Lizards.	*Eristalis vulpinus* eaten in large numbers by *L. viridis* (*A. G. Butler*).	Strong support.
.....	Eaten by *Lacerta viridis*.	.....	Strong support.
The males eaten in large numbers by young *Hylæ*.	.....	.....	Support. It would be exceedingly interesting to compare the behaviour of Lizards and birds towards the male and female insects.
Eaten by *L. viridis*	.....	.....	Support.
Eaten by all the Lizards	.....	.....	Support.
Eaten by all the Lizards	.....	.....	Support.
Eaten by *L. muralis*.....	.....	.....	Support.
.....	Eaten with avidity by the Lizards.	Well known to be the favourite food of Pheasants &c. In this case the species is *Formica rufa*.	Support.

TABLE V.

Species and Class or Order.	Protective resemblance, or habits of concealment, evasion, &c.
HYMENOPTERA.	4. IMAGINES OF OTHER INSECTS AND A FEW ARTHROPODA
Winged females of Ants, sp. ?	Colour and some of the habits appear to be protective. The gregarious habits, however, make them conspicuous, but are very important in rendering their acid secretion more formidable.
Workers of Ants, sp. ?.....	As above .....
Apis mellifica	Workers made use of in all cases. The brown colouring renders the insects somewhat inconspicuous. The comparison in this respect with the more formidable Wasp is interesting.
Andrena nigro-ænea.....	The insects bear considerable superficial resemblance to the workers of the last species.

Newman states, "always I believe on herbaceous plants, never ascending trees." In this respect Newman is mistaken, for I have frequently found the full-grown larva feeding on the leaves of plum in my own garden, and it was such an individual which was given to *L. muralis*.

I can now add my own experience of the larval habits subsequent to the period at which Newman has described them. In the winter of 1884–5, I kept a number of larvæ and watched them from time to time throughout the whole period of hybernation. As the room in which they were kept was warmed, they frequently woke up at night and fed upon the Calceolaria-leaves with which they were supplied. I was most interested in observing the extreme care with which they were concealed by day. If there were any brown leaves among the food the larvæ would always get upon these, and, not content with the harmony between their colour and that of the leaf, would force their way into furrows and folds, so that they came to lie in deep shadow and were often quite concealed. I took some pains to see what the larvæ would do when all the brown leaves were carefully removed, and I found that, by seeking the darkest corners

continued).

Experimental evidence.			Bearing upon Wallace's converse suggestion.
E. B. Poulton.	J. Jenner Weir.	Other observers.	
OF OTHER CLASSES (*continued*).			
.....	Eaten by *Z. vivipara*.	.....	Support; it seems clear that the Lizards do not much object to the secretion.
.....	Refused by all the Lizards.	.....	It may be that this secretion or the means of using it is more formidable than in the winged females.
Often seized and swallowed by Frogs; but I believe nearly always rejected in the end, and very often rapidly ejected soon after being seized, as though the animal had been stung. Often eaten by hungry Lizards; but they showed great caution in their manner of seizing and disabling the insects.	.....	A. G. Butler.—Eaten by Frogs, apparently with avidity. Well known to be eaten by Lizards, and that Spiders also catch the Bees easily and frequently.	These facts show that even an insect protected by a sting may fall a victim to enemies if hungry. The comparison with Wasps supports Wallace's suggestion.
Seized and swallowed by Frogs; but I believe nearly always rejected in the end, as above.	.....	.....	Conclusion as above.

and deepest folds among the green leaves, they were nearly as well concealed. If a leaf became rolled up at the edge, there was certain to be a larva inside. The larvæ were kept in a glass cylinder upon a plate, and the stem of the food-plant passed through a hole in the plate and into water in a stoneware vessel placed beneath. Sometimes the stem did not fit tightly in the plate, and then all the larvæ crept through the hole and rested by day upon the stem above the water, where of course it was very nearly dark. I have had very similar experience with larvæ found upon trees. I especially remember one instance in which the leaves were completely removed from the young shoots on one part of a plum-tree trained against the wall. I could not find the larva for several days, but finally detected it most carefully concealed in the folds of the single brown and withered leaf which still remained on that part of the tree.

I have now given as much information as I possess of the habits by which this larva renders its brown imitative colouring as efficacious as possible for evading the eyes of its enemies. I have gone into details in order to show that the larva belongs to a class which is the

most complete opposite of that in which the larvæ render themselves conspicuous in various ways. The experimental evidence shows, however, that the larva has a most disagreeable taste and (almost certainly) smell, so that the most ravenous of all my Lizards would not eat it. It is perfectly clear that these two methods of protection are antagonistic if present in the degree and kind possessed by this larva. One of them must be useless and merely incidental, and as it is quite certain that the highly specialized protective colouring and habits of concealment are of value to the organism, the unpleasant taste must be the useless character. And this was seen in its treatment by the Lizard, for the larva was recognized at once as something which was expected to be palatable, and was at first seized with great vigour, and it was only when the larva was injured beyond hope of recovery that its enemy recognized the unpleasant attributes and relinquished it. I witnessed the whole process; it afforded the most instructive comparison with the reluctant and hesitating way in which a very hungry Lizard would approach a highly coloured larva which it knew to be distasteful. It was quite obvious that the Lizard fully expected a palatable insect, and was greatly surprised at the unwelcome result. After the larva had bled freely, another Lizard approached, but did not taste the insect, evidently repelled by the unpleasant smell of the freshly escaped fluids. It is obvious that a larva of this kind, being unpalatable, and yet giving off no strong smell from its surface, by which to warn its enemies, belonging, moreover, to an immense group of similarly protected insects of which the vast majority are highly relished,—it is certain that such a larva can gain nothing by an unpleasant taste which can only be appreciated after fatal injury, and which is not associated with any colour, marking, or habit by which the disagreeable experience could be remembered.

We are therefore driven to the conclusion that the unpleasant quality is in this case a merely useless character, probably some incidental result of the physiological processes of digestion or metabolism. But such a condition is most important on theoretical grounds, for it at once supplies the necessary steps by which a species can change from one protective method to another. The most constant objection or difficulty which is raised against the explanation of the rise of any well-marked structure or function as due to the action of natural selection, deals especially with the initial stages. It is asked how natural selection can accumulate the earliest variations, which are (the objectors assume) of insufficient importance to act as criteria by which life and death can be settled. Darwin set the great example of giving a satisfactory answer to such objections by carefully working out one by one those cases in which especial difficulty was assumed. And here, by the instance of the larva of *M. typica*, we see at once how the difficulty of the origin of nauseous forms may be overcome; for this larva possesses a useless attribute ready-made as the incidental result of some physiological process, and at so high a stage of efficiency that there is no difficulty whatever in imagining that it might readily become an important criterion of existence,

falling therefore under the influence of natural selection. Knowing that increasing efficiency in protective measures is counterbalanced by increasing keenness and cunning on the part of enemies, it is easy to see how, as a response to an advance by the latter, a species might take advantage of such an incidental quality to adopt an entirely new line of defence. The concealment of the larvæ we are considering is evidently very successful, but if it were seen through far more frequently than at present, and yet the larvæ were always rejected with disgust, there would be more and more opportunity and necessity for the enemies to remember the experience; and the further the species varied away from the beaten path of protective colouring, the greater aid would it afford to memory, which, although that of another animal, is in this respect of far less importance for the possessor than for the larva itself. I need hardly point out that in speaking of an advance in the keenness of Vertebrate insect-eaters, I mean an advance in the power of detecting all such larvæ, so that there would always remain a large proportion of palatable species; while the new line of defence would only be open to such few of them as possess the quality of distastefulness in a marked degree. I am quite aware that there is another possible explanation of the unpleasant qualities in *M. typica*; *i. e.* that they are the remnant of a former defence by such means accompanied by corresponding coloration, &c.; but while this may explain similar facts in the case of certain other species, I do not think that it is likely to hold in the instance of *M. typica*, for the protective habits and appearance are correlated in so perfect a manner that we are compelled to assume that a very long period of time must have been covered in the attainment of so unusual and specialized a result.

It now remains to consider the other exceptions which are of less theoretical importance although of extreme interest. As the same species have occurred before under other tables, it will be well to shortly tabulate the results of all the instances among Lepidoptera in which experiments have been made upon more than one stage (see Table, p. 262).

I much hope that future experiments will enable us to extend this Table, but short as it is, it appears to point to several interesting conclusions. In the first place there is no known instance of distasteful qualities in stages later than the larva when the latter is itself palatable. This statement will doubtless be true of the great majority of species however complete be the experimental investigation, and it points to the conclusion that this method of defence arose first in the larval stage. Such a relation is to be expected; for the species is exposed to more danger and is more helpless at this period than at either of the subsequent stages. The unpleasant taste appeals to non-parasitic enemies which devour insects; but the almost complete limitation of the attacks of insect-parasites to the larval stage must bear in an important way upon the other modes of protection in this stage, tending to produce that extraordinary specialization in defensive methods which are well known to occur. The imago can escape by flight, and the pupa, if exposed, may render

Species.	Larva.		Pupa.		Imago.	
	Appearance and habits.	Edibility.	Appearance and habits.	Edibility.	Appearance and habits.	Edibility.
Pieris brassicæ	Conspicuous.	Unpalatable.	Protective resemblance (highest class).	.....	Protective resemblance at rest; strong flight.	Palatable.
Vanessa io	,,	,, (Birds).	,, ,,	Unpalatable (Birds).	,, ,,	,,
Vanessa urticæ	,,	Unpalatable (Birds); palatable (Lizards).	,, ,,	Unpalatable (Birds); palatable (Lizards).	,, ,,	,,
Anthrocera filipendulæ.	,,	Unpalatable.	Protected in tough cocoon.	.....	Conspicuous and sluggish.	Unpalatable.
Pygæra bucephala ...	,,	,,	Protective resemblance and concealed.	Unpalatable.	Protective resemblance.	,,
Orgyia antiqua	,,	,,	Protected in cocoon.	.....	(♀) protective resemblance, but *very* sluggish.	(♀) ,,
Porthesia auriflua ...	,,	,,	,, ,,	.....	Conspicuous and sluggish.	Palatable (so far as evidence goes).
Euchelia jacobææ ...	,,	,,	Protective resemblance to the earth.	.....	Conspicuous.	Unpalatable.
Cucullia verbasci ...	,,	,,	Protected in earthen cocoon.	.....	Protective resemblance.	Palatable.
Halia wavaria	,,	,,	Protected in slight cocoon; inconspicuous.	.....	,, ,,	,,
Abraxas grossulariata.	,,	,,	Conspicuous.	Unpalatable.	Conspicuous and sluggish.	Unpalatable.
Cerura vinula.....	Protective colouring (until attacked).	Palatable.	Protected in very tough cocoon.	.....	Protective resemblance, or, at any rate, well concealed.	Palatable.
Spilosoma menthastri	Exposed freely, not very conspicuous.	Unpalatable.	Protected in cocoon.	.....	Conspicuous and sluggish.	Unpalatable.
Mamestra brassicæ...	Protective colouring and habits.	Palatable.	Protected in the earth.	Palatable.	Protective colouring.	Palatable.
Tryphæna orbona ...	Protective colouring and habits.	Palatable.	Protected in the earth.	.....	Protective resemblance and habits.	,,
Tryphæna pronuba	Protective colouring and habits.	Palatable.	Protected in the earth.	Palatable.	Protective resemblance and habits.	,,

its imitative resemblance complete by entire quiescence, and it is usually effectually protected in other ways; but the larva must feed, and at the same time is sluggish in its movements, defenceless, and when palatable is more relished than any other stage, for it does not possess the hard investment of the one or the scaly covering of the other. It has also been seen that an unpleasant taste may arise incidentally at this period. Assuming, then, that the great needs of certain larvæ have been met in this way, there will be the tendency for the unpleasant quality to pass on by simple continuity into the other stages; and if these are hard pressed, there is always the possibility that such attributes may be made the starting-point of a similar method of defence for them also. Hence I believe we shall nearly always find that conspicuous unpalatable imagos develop from larvæ which are also unpalatable and conspicuous, and such a conclusion is entirely borne out by the table. But the unpleasant quality may pass on in the same way into other stages, which hold their own successfully by elaborate and perfect protective resemblances, and then there will be no tendency for the quality to be made use of, although it will always remain as a possibility should the species be worsted by its enemies in these stages. It must be remembered that the possession of an unpleasant taste by a protectively coloured species can never be injurious in any way to itself except in so far as it causes the destruction of a greater amount of insect-life, inasmuch as the part contributed by the species itself to the total destroyed does not count as food under ordinary circumstances. And the species itself remaining on the same protective lines as the great mass of palatable species, it will itself come in for a proportional share of the extra loss which follows from the fact that it is not relished as food. But so long as these unpalatable species remain in a small minority, the reaction of their own inedibility upon themselves will be inappreciable. Mr. W. Esson has kindly expressed the danger actually incurred in a mathematical form, showing that it is inappreciable when the inedible species are relatively few. If there were a practically unlimited number of protectively coloured insects consisting of two sets of species, the one set edible and the other inedible and consisting of individuals in the ratio of 100 : 1, it is reasonable to suppose that in any number n of captures there will be killed of each set a number of individuals proportional to the numbers in the sets themselves; *i. e.* of the edible $\frac{100n}{101}$ and of the inedible $\frac{n}{101}$. The insect-eaters will go on catching the insects until the edible $\frac{100n}{101}$ becomes equal to the number required for their food—a. Therefore $\frac{100n}{101} = a$ and $n = \frac{101a}{100}$; therefore there are caught of the inedible species $\frac{n}{101}$, that is $\frac{a}{100}$.

Considering the above-mentioned exceptions among the imagos rather more in detail, it would certainly be difficult to find any species with an appearance more completely the opposite of that produced by the typical warning coloration than the imagos of *P. bucephala* and *O. antiqua*. The special character of the imitative resemblance

in the former has been previously alluded to. A friend has raised the objection that the moth imitates a piece of twig *cut* cleanly at both ends, an object which cannot be found in nature unassisted by art. The reply of course is that the purple and grey colour of the sides of the suggested cylinder, together with its pale ochreous ends —the one appearing to be cut transversely, the other obliquely across— present a most perfect resemblance to wood, with that particular condition of texture induced by decay, in which alone the tissue will break shortly and sharply as if cut, on the application of slight pressure or the force of an insignificant blow. *In coitu* the stick-like appearance is admirably preserved, the two insects looking like a single twig (*Newman*). It was clear from the energetic and instantaneous attacks made on these moths, that the Lizards expected them to be palatable and that the unpleasant quality is incidental and useless. It was very interesting to observe that the continuity of the unpleasant properties through the different stages in this species is accompanied by a gradual lessening in their powers. The larva was certainly disliked far more than the other stages, and the pupa seemed to be more neglected than the imago, the latter being eaten in large numbers, although often after preliminary tasting and temporary rejection. This fact also favours the explanation given above of the origin and meaning of the unpleasant qualities in the two terminal stages.

In the case of *O. antiqua*, we have a most inconspicuous insect with the same unpleasant taste. Here also the same explanation probably holds good as far as the origin of the qualities is concerned, for we have previously seen that its most brightly-coloured and freely exposed larva was disregarded by all the birds. In this case I do not yet feel certain that the property may not be of some value to the female imagos; for it would be impossible to find a more helpless insect, without even the power of attempting to escape by walking. More observations are greatly needed, and it would be especially interesting to ascertain whether the quickly-flying males are equally disliked as food.

The pupa of *P. bucephala* has been already alluded to. Confirmation is, I think, needed of Newman's statement that fowls eat this pupa freely, for the dislike of the Lizards was extremely marked, and as a rule these animals are less delicate than birds. The pupæ of *V. io* and *V. urticæ* possess the highest form of protective resemblance; and here, again, Jenner Weir's observation, I think, should be repeated, as the Lizards acted so very differently with the latter species. Is it quite certain that the birds were aware of the presence of these generally motionless pupæ in Jenner Weir's experiments?

The consideration of the fourth subdivision of the list, including species of Arthropoda other than the Lepidoptera, enforces very strongly the conclusions of the rest of this paper,—that defensive habits and structures may exist in almost any kind of combination, so that we find plenty of instances of the co-existence of unpleasant attributes with protective resemblance, as well as with a "warning" appearance.

Just as it was considered to be probable that warning-colours possess a sexual value for the species concerned, so it is probable that the most extreme cases of protective resemblance also have a similar significance. And in fact, when the most specialized instances of the latter kind are detected and are looked at in themselves, they are often seen to possess great beauty, which is absent from the objects they protectively resemble. To take an extreme case, the imago of *Melanthia albicillata* sits upon the upperside of a leaf in the usual attitude of the Geometers, with its wings extended as if "set," and in such a position its creamy-white ground-colour and dark lines and blotches are very conspicuous, but most forcibly suggest the appearance of bird's excrement which has fallen on to a leaf from a great height, and has therefore been spread out into a large wide patch. But when the insect is detected and examined, it is seen to possess the greatest beauty. Thus Mr. Beauchamp says of it:—"The perfect insect, when bred, seems to me almost without a rival for purity and exquisite delicacy of design. I should doubt whether in the range of natural objects a more beautiful line is to be found than that exquisite cool grey streak upon the rich creamy ground of the fore wing" (Newman's 'British Moths,' p. 156). While entirely agreeing with this description, we should all maintain that it is very far from applying to the object suggested by the Moth, and which it nevertheless resembles very faithfully. And it is probable that in all cases the appearance of a sexually mature insect possesses this among its other meanings.

Thus I believe that the brightly-coloured underwings of the genus *Tryphæna* have the same significance as those of *Catocala* and of *Sphinx* and *Smerinthus*, and the same significance as the bright colours of the uppersides of both wing in most Butterflies, which are also concealed during rest. But in *Tryphæna* alone among these the bright sexually selected adornment has another meaning as well, and has also come under the independent action of natural selection. For the black and yellow colours of these wings, together with the colours of the undersides of both wings, seen during their rapid vibration in flight, greatly aid the protective resemblance to a dead leaf whirled along by the wind. And yet the very similar arrangement of *red* and black on the upper and undersides of the underwings in *Catocala* are comparatively non-protective and seem to have almost purely sexual significance. If, therefore, these brilliant colours of *Catocala* were modified by natural selection as a response to some unusual activity on the part of its foes, if they became yellow and black instead of red and black, and the habits were correspondingly modified, we should have no reason to conclude that they had in consequence lost their sexual significance, and there is no reason for forming such a conclusion in the case of the genus *Tryphæna*.

Jenner Weir has suggested that these brightly-coloured underwings have another protective meaning—that they are conspicuous, and hence form the mark of an enemy, and yet when seized they readily give way without doing harm to the insect. Again, he

suggests that the enemies are startled by the sudden manner in which the bright colours are displayed; but I am not aware that a similar significance has ever been attributed to the bright colours of Butterflies suddenly seen when the wings are opened. The former suggestion probably holds, for I think the margin of the underwings is more commonly found to be notched than any other part of these insects when captured. But the primary significance of such bright colours, concealed in the protective attitude of rest, must be the same as those of Butterflies, and I should attribute the same meaning —of sexual adornment—to the brilliant colours of the underwings of the Grasshoppers of the genus *Œdipoda*, also alluded to by Jenner Weir (see Trans. Ent. Soc. Lond. 1869, pt. i. p. 23).

Conclusions.

The following are the general conclusions arrived at by the consideration of the experimental data tabulated in this paper:—

1. The extremely specialized defence of the larval stage follows from its delicate anatomical construction and the necessities which are imposed on it as the great feeding-stage.

2. Highly conspicuous insects nearly always possess some unpleasant attribute, *i. e.* a disagreeable taste or smell in the tissues and fluids of the body, or (in the case of the smell) discharged from special glands; irritating hairs; or stings.

3. The conspicuous appearance may be due to strongly-contrasted colours, the presence of hairs or tufts, and the attitude in which the body is held, and to gregarious habits, or attention may be attracted by violent movements which take place when an enemy appears.

4. In a small number of cases a highly conspicuous appearance has not yet been shown to be attended by any unpleasant attribute.

5. In the various species in which a conspicuous appearance is produced by colour and marking, the same colours and patterns appear again and again repeated. In this way the Vertebrate enemies are only compelled to learn a few types of appearance, and the types themselves are of a kind which such enemies most easily learn. Furthermore certain appearances are especially impressed on the vertebrate foes by highly aggressive insects, feared because of stings &c.; and hence there is especial advantage in any approximation to such types. Again, the selected type of conspicuous appearance also depends on the (probably protective) colours which existed at the time when the conspicuous appearance first commenced (these can be determined with a great degree of probability in some few cases).

6. In a relatively few cases aggressive forms among the Vertebrata (Serpents) are mimicked, although such an appearance is pure intimidation, for the insect is quite harmless.

7. It is not uncommon for an insect to be protectively coloured but when detected to assume a terrifying attitude, and in some cases to take up offensive measures (discharge of irritating fluid, &c.).

8. A few, probably transitional, forms may be unconcealed, and yet not very conspicuous; these may possess unpleasant qualities or may be eaten readily.

9. The likes and dislikes of insect-eaters are purely relative, and if pressed with hunger the most disagreeable and highly conspicuous insects may be eaten. Hence probably the relatively small number of species which adopt such a means of defence.

10. It seems probable that when one Vertebrate eats an unpleasant insect, and another refuses it, the former has conquered its prejudices, having originally disliked the insect.

11. In the sexually mature forms warning colours can be distinguished from sexual colours by their distribution on the surface of the body, by the way in which they are displayed in flight, by their type of pattern, and the colours employed. The sexual colours and patterns are *beautiful*, the others *conspicuous*. Nevertheless, to the modified taste of a highly conspicuous insect, the warning colours probably possess value as sexual adornments.

12. The conspicuous appearance has relation to the injury which would be inflicted by the experimental "tasting" of certain enemies, *e. g.* Birds and Lizards; but nevertheless, other enemies, which do not inflict injury in tasting, *e. g.* Frogs, have taken advantage of the warning colours to a limited extent.

13. Insects which evade their enemies by protective resemblance and attitude, rapid movements, or habits of concealment, &c., are generally palatable, but they may often possess an unpleasant taste or smell which may or may not protect them from enemies.

14. In a very small number of species the most perfect form of protective resemblance may coexist with a most unpleasant taste.

15. Mere size alone may protect a species against certain of its smaller foes.

16. Comparing the different stages in Lepidoptera, unpleasant attributes appear to arise in the larval stage, and they then often pass through the two other stages attended or unattended, in one or both, by warning colours.

17. The most highly specialized protective colours probably also possess value as sexual adornment.

Considerably over 100 species or stages of insects have been experimented upon, and the results are described in the Tables given in this paper. Looking at these results as a whole, it is seen that the various defensive measures may exist in almost any combination, and that the present condition of a species is in large part an outcome of the means of protection in past struggles. Just as in a long-contested battle the same position may be taken, lost, and retaken, but never held a second time with quite the same significance as before, because of all that has happened as a result of the previous occupation and of all that has happened since in other parts of the field, so in the ever-changing relations between a species and its enemies the structural and functional means of defence may be taken

up, abandoned, and again taken up, but never in quite the same combination or with quite the same defensive meaning.

APPENDIX I.

J. Jenner Weir's Diary of Observations during 1886.

The Lizards with which the following experiments were made were :—

Lacerta viridis, two specimens, ♂ & ♀.
Lacerta agilis, two specimens, ♂ & ♀.
Zootoca vivipara, one specimen, ♀.

May 31.—*Lacerta viridis* ♂ seized the larva of *Abraxas grossulariata*, and immediately dropped it, afterwards licking its jaws as if to remove the unpleasant taste; the ♀ of the same species then examined the caterpillar and rejected it.

June 4.—*Lacerta viridis* ate the imago of a species of *Chrysopa* twice during the day; this was the more remarkable, as these insects are peculiarly malodorous.

June 9.—*Lacerta viridis* ate two larvæ of *Clisiocampa neustria*, but afterwards refused to eat more.

June 11.—*Lacerta agilis* ♀ after much hesitation swallowed a larva of *Clisiocampa neustria*.

June 12.—Larvæ of *C. neustria* and *Porthesia similis* (*auriflua*) refused by all.

Lacerta agilis ♀ ate one larva of *Abraxas grossulariata*.

June 13.—The imago of *Tipula oleracea* eaten by ♀ *Lacerta viridis*.

June 14.—Larva of *Abraxas grossulariata* tasted by *Lacerta viridis* ♂, and rejected.

June 15.—*Lacerta viridis* ♂ ate *Clisiocampa neustria*; *Lacerta agilis* ♂ bit the larva of *Abraxas grossulariata*, but refused to eat it, and afterwards rubbed his nose and mouth against the moss as if endeavouring to remove a disagreeable taste.

Cocoons of ants were eaten with avidity.

July 1.—*L. viridis*, *L. agilis*, and *Zootoca vivipara* all ate Aphides.

July 9.—Imagines of *A. grossulariata* refused by Lizards.

One imago of *Porthesia similis* (*auriflua*) eaten.

Aphides scarcely noticed.

July 31.—Imagines of *Halia wavaria* and *Camptogramma bilineata* eaten.

Spiders eaten greedily.

August 2.—Imago of *Abraxas grossulariata* refused after having been seized.

August 6.—*Lacerta agilis* ate unwillingly, and *L. viridis* refused the larvæ of *Pygera bucephala*.

Zootoca vivipara ate winged ♀ ant, but all the Lizards refused the neuters.

August 11.—Imagines of *Eristalis* and of *Syrphus* eaten by all the Lizards voraciously.

August 12.—One *Pygæra bucephala* larva was eaten, but this species generally allowed to crawl about the cage unnoticed.

August 27.—An evil-smelling inconspicuous Hemipteron refused after tasting.

August 30.—Lizards refused to eat the gooseberry sawfly.

August 31.—Lizards ate common earwig and imagines of *Tryphæna pronuba*, *T. orbona*, and *Amphipyra pyramidea*.

Sept. 5.—*L. viridis* ♀ killed, but refused to swallow a humble-bee (*Bombus*).

Sept. 14.—Lizards ate imagines of *Mamestra brassicæ*, *Pieris brassicæ*, and *P. rapæ*.

Sept. 27.—*Zootoca vivipara* ate larva of *Tryphæna pronuba*.

Oct. 2.—Larvæ of *Tryphæna arbona* eaten, and imagines of *Anchocelis pistacina* seized and eaten greedily, but apparently swallowed with difficulty.

Oct. 4.—All the Lizards refused the imago of *Vanessa urticæ*.

Mr. Jenner Weir also informs me that the common Muscidæ were eaten with intense relish, their larvæ and pupæ being also eaten.

APPENDIX II.

E. B. Poulton's Diary of Observations during 1886.

May 8.—About this date one larva of *L. quercus* was offered to *L. muralis* and *L. viridis*, but it was untouched, although allowed to remain many days in the cages. One imago of *Pieris rapæ* was eaten. One imago of *Dasychira pudibunda* (♀) was seized and eaten directly it was seen to move (*L. muralis*).

One larva of *Mania typica* was eagerly seized by two individuals of *L. muralis*, being detected while it was rolled up and motionless (feigning death). The larva was shaken and bitten, but it was not swallowed, and the Lizards rubbed their jaws upon the wooden floor of the cage, an evident sign of distaste. When the larva had been thus wounded another Lizard came up and inspected it closely as if it were going to bite, but soon retired without touching it. It seems probable that this last Lizard was warned by the smell of the larval fluids which had escaped after it had been wounded.

Four pupæ of *Pygæra bucephala* were introduced (*L. muralis*) and were bitten, but at once relinquished with the signs of distaste described above.

Earthworms were eaten with great avidity by all the species of Lizards.

May 9.—Five imagos of *P. rapæ* were eaten, two of them immediately. One imago of *Pieris brassicæ* was eaten at once, being pursued by two or three Lizards (*L. muralis*).

Two imagos of *Pieris napi* were immediately seized and eaten.

One imago of *Trichiosoma lucorum* was eaten at once by *L. muralis*.

May 18.—One imago of *Chloephora prasinana* was seized and eaten the instant it was seen to move but not before (*L. muralis*).

May 19.—One imago of *Gonoptera libatrix* was at once detected

by two Lizards even when motionless; it was seized and eaten with great avidity (*L. muralis*).

One Noctua pupa (found when digging in the garden; almost certainly that of *Mamestra brassicæ*) was instantly seized, slightly crushed, and swallowed with great avidity (*L. muralis*). It was interesting to note the great difference between the treatment of this pupa and that of *P. bucephala*.

May 21.—One imago of *Anthocaris cardamines* (♀) was seized and eaten immediately (*L. muralis*).

May 30.—Two imagos of *C. prasinana* were eaten directly with avidity. A few larvæ of *Odonestis potatoria* were placed in the cage of *L. muralis* a day or two before, and after long delay had disappeared by this date. Two were offered to the same Lizards on this day, and one was taken at once, the other being untouched for a long time. It is quite evident that the species is disliked, but that the Lizards will eat it if they are hungry.

Several pupæ of *P. bucephala* were introduced; from one of them an imago emerged almost immediately, and was at once seized and then relinquished by two or three individuals of *L. muralis*, but it was finally eaten, although evidently unpalatable. The pupæ were not touched on this day.

One imago of *P. rapæ* was eaten at once.

One imago of *P. brassicæ* was eaten, but not at once, by *L. muralis*.

June 2.—One imago of *P. rapæ* was eaten at once by *L. muralis*.

June 4.—One pupa of *Tryphæna pronuba* was eaten directly by *L. muralis*.

One imago of *Euplexia lucipara* was eaten directly by *L. muralis*.

Two imagos of *Hepialus lupulinus* were eaten directly by *L. muralis*.

One imago of *P. bucephala* was seized at once but soon relinquished by *L. muralis*.

June 6.—The *P. bucephala* imago introduced on June 4th had now disappeared; another was offered on this day and was at once seized and eaten by *L. muralis*.

The larvæ of *O. potatoria* had now disappeared.

Three imagos of *P. rapæ* were eaten at once by *L. muralis*.

One imago of *P. brassicæ* was eaten immediately by *L. muralis*.

After this last date the various species of Lizards to which insects were offered were always accurately noted, and were indicated by the numbers I., III., IV., V., and VI. placed upon their respective cages, and which contained the following species:—

I. *Lacerta muralis* (var. *tiliguerta*), about a dozen fine specimens.

III. One ♀ *Lacerta viridis* and two ♂ of the same species: all fine individuals.

IV. *L. muralis*, var. *tiliguerta*: about half a dozen full-grown specimens.

V. A few small individuals of *L. muralis* (more than one variety).

VI. One ♀ *L. viridis*, a very fine specimen, and one full-grown Gecko (*Tarentola mauritanica*).

June 11.—I. Four imagos of *P. bucephala* were introduced, one was seized directly but relinquished; ultimately all four were eaten.

Four larvæ of *Abraxas grossulariata* were untouched.

III. Two imagos of *Cerura vinula* and four of *P. bucephala* were all taken ultimately. These Lizards (*L. viridis*) were very shy, and hardly ever seized an insect before an observer; being quite unlike *L. muralis* in this respect.

Two larvæ of *A. grossulariata* disappeared, but they may have escaped, being small larvæ.

IV. Five larvæ of *A. grossulariata* introduced; I saw one severely bitten, in fact chewed for some time, but it was ultimately relinquished. One larva of *C. neustria* was also added, and with the *A. grossulariata* could not be seen on the next day. It is possible that they may have escaped, and I do not attach importance to their absence, unless escape was impossible. One imago of *P. bucephala* was ultimately eaten.

V. Two imagos of *Amphydasis betularia*, one of *Mamestra persicariæ*, one of *M. brassicæ*, and one pupa of *Plusia gamma* were introduced and all eaten (I witnessed the capture of one *betularia* and the *persicariæ*). Four larvæ of *A. grossulariata* were untouched.

VI. Two imagos of *P. bucephala* were eaten ultimately.

June 13.—V. One imago of *Acronycta psi* was ultimately eaten.

June 15.—I. Three imagos of *P. bucephala* were all eaten by the next day.

III. Six imagos of *P. bucephala* were introduced, and five were eaten by the next day.

V. One imago of *A. cardamines* (♀) was eaten by the next day.

VI. Four imagos of *P. bucephala* were introduced and three were eaten by the next day.

In these cases the insects may have been eaten at any time between their introduction and the next day, when the next observation was taken.

June 17.—I. One imago of *Sphinx ligustri* was introduced and untouched.

V. One imago of *Hadena oleracea* and one of *A. psi* were eaten by the next day.

June 18.—I. The *S. ligustri* introduced yesterday was resting on the upper part of the cage out of reach of the Lizards; it was again placed on the floor of the case, but remained untouched.

June 19.—III. The *S. ligustri* was still untouched in I. cage, and it was therefore removed and placed in III. When the next observation was made, a few hours later, it was entirely eaten except a piece of one wing.

I. Two full-fed larvæ of *Tæniocampa gothica*, found feeding upon *Aconitum napellus*, were introduced to see if they were affected as food by the exceedingly poisonous properties and strong taste of the plant upon which they had been feeding. It seemed possible that the undigested food in the larval digestive tract might be harmful to the Lizards, even if the insects made no further use of the properties

of their food for purposes of defence. However, the Lizards fought eagerly for the larvæ, and the two successful ones were separated from the rest and remained perfectly healthy.

June 21.—I. An imago of *Smerinthus populi* was eaten by the next day, having been seized at once.

III. One imago of *S. populi* and two cockchafers (*Melolontha vulgaris*) were introduced; by the next day the former and one cockchafer had been eaten.

June 25.—I. One imago of *S. lubricipeda* was eaten at once, and many imagos of *P. bucephala*.

III. One imago of *S. ligustri* was eaten in a few minutes.

July 1.—I. One imago of *S. lubricipeda* and one of *Macroglossa fuciformis* were soon eaten, the former at once. The Lizard did not seize the *M. fuciformis* with any caution, as if afraid of a sting.

July 4.—I. Three pupæ and two larvæ of *Vanessa urticæ* were eaten at once; one larva of *P. auriflua* was seized at once and chewed for some time, but it was ultimately relinquished, the Lizard seeming to be much irritated by the hairs, and continually opening its mouth. Two imagos of *Ennomos angularia* and one of *A. psi* were taken at once. One unnamed larva of a Sawfly was seized and relinquished, but apparently taken again.

IV. Two pupæ of *V. urticæ* were soon taken.

V. Three pupæ of *V. urticæ* were soon taken.

VI. One imago of *S. ligustri* taken.

August 14.—I. Six imagos of *Vanessa io* and about eight of *V. urticæ* were introduced, and many were seized at once; but the Lizards were apparently not very eager after them, although they were hungry. However, in twenty-four hours all had disappeared except one *V. io*, which had got into an inaccessible place, but when brought down it was eaten at once.

August 16.—I. A few larvæ of *V. urticæ* were eaten at once. Two larvæ of *Euchelia jacobææ* were seized at once but relinquished, the Lizards being very hungry. A few hours afterwards they had disappeared and were very probably eaten; but I do not feel able to speak with confidence, as the larvæ are small and might possibly have escaped.

September 6.—On this date *L. muralis* and *L. viridis* were taken to Birmingham and offered distasteful larvæ at a meeting of the Biological Section of the British Association. One larva of *P. bucephala* was placed in the cage of *L. muralis*, and although it was often very severely bitten and for some considerable time by many of the Lizards, it was not eaten. For a day or two before this date the same species of larva had been placed in the cages of *L. muralis* and *L. viridis*, and some of them had disappeared, so that I believed that they must have been eaten. Subsequently I was able to confirm this suspicion, for when I was removing the individuals of *L. muralis* from the travelling cage (Sept. 7), I found the fæces of one of them upon the floor, the excreta *consisting entirely of a partially digested larva of P. bucephala*.

I also offered (Sept. 6) the same species of Lizard a number of larvæ of the Sawfly (*Crœsus septentrionalis*), and although the Lizards seized them eagerly at first, they soon rejected them with every sign of disgust, the jaws being rubbed against the floor of the cage to remove as far as possible every trace of the unpleasant taste. However, on the railway journey from Birmingham to Oxford (Sept. 6) I actually saw a hungry Lizard seize one of these larvæ, and with much hesitation reluctantly swallow it. I was surprised at this behaviour, for earlier in the summer I had certainly seen these same larvæ devoured with apparent avidity by nearly all the Lizards. On one occasion also I placed the conspicuous pupa of *Abraxas grossulariata* in the cage of *L. muralis*. I subsequently found that it had been bitten, and as all its contents were gone it seems certain that it had been at any rate partially eaten. I have also offered the imago of this species to the Lizards, but it has always been refused after tasting in some instances. Furthermore, immense numbers of pupæ and imagos of *Vanessa urticæ* were eaten by all the Lizards at various dates towards the end of August and beginning of September, while early in the summer humble-bees (*Bombus lapidarius* &c.) were sometimes eaten by *Lacerta viridis*, and the common hive-bee (worker) was sometimes eaten with considerable caution by most of the Lizards. Common wasps (queens and workers), on the other hand, were invariably undisturbed ; and this was also the case with *Nomada marshamella*. Cockroaches were always eaten with avidity by all the Lizards, as well as the common species of Muscidæ, with their larvæ and pupæ. *Coccinella septem-punctata* was invariably refused without tasting. The Carabidæ—*Carabus hortensis* and *Omaseus melanarius*—were eaten readily. The Isopod (*Armadillo vulgaris*) was also relished.

Experiments with the Frogs (*Hyla arborea*, var. *meridionalis*) were less numerous and systematic; but they yielded some very interesting results:—

May 7, 1886.—A queen wasp was put in the aquarium, and immediately a Frog sprang at it and drew it into its mouth, but instantly recognizing (apparently by the tactile sense) the danger, released the insect. It is possible that the Frog was stung, but the whole process, capture and release, was so rapid that it is very likely that the animal escaped. As soon as the wasp was free a second Frog behaved in precisely the same manner, and after this a third. After this I did not see the wasp again attacked, and it was left in the aquarium for twenty-four hours.

May 9.—One imago of *Pieris napi* taken instantly.

May 13.—One imago of *A. cardamines* (♀) taken instantly by one Frog after being refused by others.

May 29.—One imago of *A. cardamines* (♀) eaten at once by one Frog after having been refused by others.

One imago of *Orgyia pudibunda* (♂) eaten at once by one Frog after having been refused by others.

June 6.—Two imagos of *E. jacobææ* were eaten at once, one directly after the other, *by the same Frog*, so that the taste could not

have been unpleasant. However, they were evidently indigestible, for next day both were found floating in the aquarium.

One larva of *A. grossulariata* was refused after being just tasted by one Frog.

These are all the regular notes made upon the insects eaten by the Frogs, but in addition to the above various other larvæ and imagos were given to them. The following imagos were eaten:—*E. angularia*, *V. urticæ* (both these in great numbers, although they were often refused by individual frogs), *Acronycta psi*.

The following larvæ were also eaten:—*Phlogophora meticulosa*, and the hymenopterous *Crœsus septentrionalis*.

Although wasps were refused, the common hive-bee was eaten, together with other species of bees (*e. g. Andrena nigro-ænea*) and many species of Diptera (*e. g.* common species of *Musca*, *Eristalis*, and *Syrphus*, *Bibio marci*, &c.) and of spiders (*e. g. Epeira diadema*, *Tegenaria domestica*, &c.). All of these were relished and eagerly sought after except the bees, which were generally swallowed, but in most cases rejected afterwards and were found floating in the aquarium. Very often I saw the bees (*Apis* and *Andrena*) liberated after being held in a Frog's mouth for some seconds, and as soon as the animal began to reject it most violent and active efforts were made, especially with the tongue, in order to get rid of the insect as rapidly as possibly. From the sudden and spontaneous way in which the insect was often rejected after being held in the mouth for some seconds, I was led to believe that the Frog was stung. Earthworms were eaten by some of the Frogs, but apparently without relish, and the majority refused them altogether, and the same was true of the larvæ of the commonest Muscidæ. *Coccinella septem-punctata* and *C. bipunctata* were invariably refused. Cockroaches, Earwigs, and *Aphis hederæ* were eaten, the latter by very young Frogs.

2. An Account of the Fishes collected by Mr. C. Buckley in Eastern Ecuador. By G. A. Boulenger, F.Z.S.

[Received February 7, 1887.]

(Plates XX.–XXIV.)

The rich collections brought over from Ecuador by the late Mr. Clarence Buckley in 1880 contained a large number of highly interesting and well-preserved Fishes obtained at three localities, viz. Canelos, Sarayacu, and Pallatanga. On the arrival of the collection a set of all the species was selected and retained for the National Museum. The duplicates having been sold by the well-known dealer Mr. Gerrard to other institutions, principally to the Vienna Museum, some of the novelties have already been described by Dr. Steindachner.