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The Colouring Matters of Leaves and Flowers.

By PHILIP SEWELL.

(Read 8th March, 12th April, and 10th May 1888.)

[The following paper was, for convenience, divided into three parts, the first dealing with the physical and chemical properties of this class of colours; the second with colour changes; the third with the various hypotheses which, more or less recently, have been put forward to account for colour phenomena.]

The paper is an expansion of one on Floral Colour, read in December of last year to the Botanical Society.]

PART I.

A. Physical Properties.

Their different physical characters were, naturally enough, those that first attracted the attention of botanists who wished to classify the various colours of plants. Many workers, since the time of De Candolle, who divided plant-colours into solid and fluid (xanthic and cyanic), have pointed out the necessary imperfection of a purely physical classification of them, and at the present time solubility, the appearance of particular spectra, and, so far as can be ascertained, chemical composition, all enter into account in any attempt at a natural grouping together of colouring matters of plants.

If we inquire as to what is the nature of the difference between so-called solid and fluid colours, we find that the solid are associated with a protoplasmic corpuscle of varying size and shape, and may, therefore, be called by the better name, used by Vines, "fixed" colours. Pringsheim states that some of these protoplasmic corpuscles have in their surface small pits, in which is mechanically retained the oily or viscid coloured fluid—the chlorophyll or the etiolin, as the case may be. The fluid colours are commonly dissolved in the cell-sap, although at times, as we shall see, they pass into the cell-wall or into the solid cell-contents, or, and this not uncommonly, occur crystallised within the cell.

The fault of De Candolle's classification, which of course was a purely arbitrary one, is clearly seen in this, that he regarded yellow colours as solid colours distinctively, blue and

red as fluid distinctively. Hence, when it was recognised that yellow commonly exists as a fluid colour, and that red, and even blue, are at times attached to solid bodies, some other more natural arrangement was required. The real relationship of the colours is brought out in the assertion of Schimper (in 1885) that, in the different stages of developing colour-corpuscles, there may be found all shades from pale yellow, or green, to brilliant carmine; whilst at the same time there is transition of form of the retaining corpuscle. "The colouring matters of leaf and flower affect a series of states connected with and passing into each other," says Bonnier. We have to think of evolution among coloured products in the cell; of the yellow of etiolin, as indicated fully in Vines' *Lectures on Physiology*, becoming transformed into the green of chlorophyll; or, on decomposition, passing into yellow or red, either retained by the corpuscle of protoplasm; or, most commonly passing (the yellow as xanthophyll) into the cell-sap. We come, indeed, to regard the fixation of colouring matters as a sign of specialisation—that is, of a division of labour by the protoplasm of the cell. Amongst the lowest Cryptogams it is present as a viscid fluid distributed throughout the whole of the homogeneous protoplasm of the cell; amongst the Diatomaceæ, or as in *Spirogyra* amongst filamentous Algæ, it is present as bands in the protoplasm lining the interior of the cell-wall. Its association in the higher plants with the numerous distinct corpuscles, capable of being moved in the cell by the investing layer of protoplasm, is a clear case of differentiation; the corpuscles are isolated as the special portions of the protoplasm which effect the synthetic formation of carbohydrates.

The development of the chlorophyll and of its corpuscle (the chloroplast) has of late years, mainly through the observations of Schimper and Meyer, been very distinctly followed. The chloroplasts arise from colourless plastids, which have been traced in all young meristem, and even in the embryo-sac of various plants; they divide directly, and, at maturity, a yellow colouring matter, etiolin, appears as the result of the reduction of part of the protoplasm of the corpuscle. It is this etiolin which on exposure to light may become green.

It is interesting to notice, that a starch-grain in the cor-

puscle, obtained by it by the reduction of proteids in the cell, disappears as the etiolin is formed, being in part used in building up the protoplasm of the corpuscle, which protoplasm in turn goes to the production of the colour-substance.

As to stages subsequent to the production of the chlorophyll, Schimper and Baccarini have recorded that, from the round chloroplast may be formed a body of crystalline character, and of red or yellow colour, invested by a layer of protoplasm.

Evident conditions of degradation are commonly seen in fading leaves, where the chlorophyll-corpuscles either undergo disintegration, the whole leaf becoming brown, or collect together into amorphous masses; these, although at times differently coloured, are most commonly rendered yellow by the presence of xanthophyll. This xanthophyll is the substance into which the chlorophyll has chiefly altered.

Messrs Martin and Thomas have recorded several interesting observations as to the condition of the cells in leaves which, as in autumn, are undergoing colour-change. When red, the denser cell-contents have mainly disappeared, the colour being free in the cell-sap; when yellow, the colour is chiefly in the amorphous masses, the change evidently not having proceeded so far. The subsequent brown stage is one of complete decomposition, without any signs of vitality such as are exhibited with the other colours.

Colours occur most commonly as follows:—

White.—Either as plastids of an almost transparent or a very pale yellow colour, when the whiteness is not of a pure kind. Whiteness, however, is generally due to the presence of air in the tissue of which the part consists, and this allows of nearly total reflection; the cause being exactly similar to the cause of the whiteness of snow. Rose-coloured geraniums example the combination of cells containing air with others underneath containing red colouring matter.

Yellow is fixed as etiolin, in leaves or in certain flowers (it has an evident similarity with Krukenberg's "lipochromes"); or as fluid xanthophyll in leaves or many (? most) flowers.

Red appears at times attached to ordinary chromoplasts, at times in the form of crystals or globules, either with or without an investing layer of protoplasm; more generally it occurs in the cell-sap produced immediately, or mediately

from chlorophyll or etiolin. In many cases red, especially where tannin is present, is known to result from the decomposition of glucosides, for example, in certain roots.

Blue is very rarely fixed. It is probably a derivative of red in all cases.

Violet, like orange and scarlet, is produced by the mixing of certain of the colours already mentioned in the same tissue, for instance, where cells containing fixed yellow have fluid red in the superposed cells.

Black is a result of the concentration of violet pigment.

Brown is due to amorphous decomposition-products, or to the presence of red and yellow pigments in the cells.

Variegated colours are often due, according to Engelmann, to localised colours in the walls of the cells.

A physical property of chlorophyll as of allied colours is its fluorescence. This property is not shared by etiolin, from which, as we have seen, all the chlorophyll-colours are produced. It is a property of many vegetable colours, and may be artificially produced by the addition of alcohol to the colourless fluid of the pellucid spots of *Hypericum*, which become brilliantly red as well as fluorescent.

At the present time a large amount of information regarding colours, as observed through the spectroscope, has been collected. Etiolin, chlorophyll, and xanthophyll have each a characteristic spectrum. The position of the absorption-bands in chlorophyll is materially changed when there is the least trace of acid present; similarly they are distinctively changed with an alkali.

More or less suggestive facts, such as the following, have been obtained—that the spectrum of fresh leaves submitted to sunlight changes in appearance, and ends by giving the spectrum of chlorophyll that has been acted upon by acids; that the spectrum of the yellow matter of dead leaves and of certain flowers is the same as that of xanthophyll; that the processes of assimilation and transpiration are variously modified according as they are effected in rays from one or another part of the spectrum.

It must be borne in mind, however, as was pointed out by M. Chaubard, in 1873, that the spectrum of chlorophyll may vary in the same plant, according to age, climate, tem-

perature, exposure of soil, and also according to the nature of the solvent in which it is held. Although corrections are now carefully made, mistakes are only too common, from errors in observation with the spectroscope, but it appears that a similar spectrum is not a certain indication of an identically similar substance, inasmuch as Sachsse has observed allied colours differing in the amount of carbon they contained, yet exactly alike in their spectra. The analysis, therefore, which alone will be conclusive as to the true relationship of these colours, lies with the chemist.

B. *Chemical Properties.*

Owing to the large mass of literature relating to chlorophyll, and in view of the certain relationship which has been detected by Schimper between it and the variously coloured chromoplasts, it is necessary for us to refer in some detail to the chemical properties of this the most important of all the colouring matters.

The first difficulty met with as to its composition is that about which so considerable a conflict has been waged—whether it should be regarded as a definite chemical substance or a mixture of several substances.

According to Vines, Pringsheim, and others the probabilities are in favour of its being a definite substance. Etiolin, however, is always present with it in the cell, and there is most commonly more or less of xanthophyll. Etiolin, as we have seen, is chlorophyll in the process of formation—xanthophyll is generally regarded as a product of its decomposition. Etiolin, as asserted by Hansen, exists in wheat-leaves in the proportion of 1 to 100 of the chlorophyll; xanthophyll, at times, as in autumn leaves, or as among the Diatomaceæ, may take the place of, or quite obscure, the chlorophyll.

Many observers, notably Sorby and Sachsse, have, on the separation of the chlorophyll from the leaf, found several other colouring matters in the solution which are distinct from it. These are generally regarded as products of the decomposition of chlorophyll, due to its removal from the cell. Sorby distinguished seven, three of which he called xanthophylls; Sachsse distinguished nine, five of which were

green and four yellow. The green contained nitrogen and a variable amount of carbon, from 66 to 72 per cent.; the yellow were destitute of nitrogen, containing from 66 to 71 per cent. of carbon, and the colours of the yellow series varied from pale yellow to yellowish-brown. The fact of the existence of such a definite series of colours so closely related, which, as Sachsse shows, differ from one another chemically, without having distinct spectra, may point to an alteration continually taking place in the constitution of the chlorophyll. It is not necessary to suppose that these substances were all produced as a result of the dissolving out of the chlorophyll.

Is it not a feasible supposition, that just as we now recognise etiolin as a step in the formation of chlorophyll, and xanthophyll as a step in its decomposition, so we may regard the individuals of these series determined by Sachsse as other steps still more close to one another? We may thus perhaps come to regard the condition of the chlorophyll in the plant as really analagous to the condition of the protoplasm from which it is derived; for just as there is now recognised in protoplasm a continually ascending and descending series of albuminoids, so we may recognise in the green colouring matter, with its distinct spectrum, a series of more or less stable compounds ever increasing and decreasing in complexity. These, under varying conditions, may be expected to alter in their relative proportion to one another in the cells of the plant, and may account for the varying composition of chlorophyll according to the many different analysts who have given us the results of their researches.

Pure chlorophyll has never been obtained, although many have supposed for a time that they had extracted it for analysis. Gautier and Hoppe-Seyler obtained by evaporation green crystals of a substance which they termed chlorophyllan, because of the ash present; for this Gautier suggests the formula $C_{19}H_{22}N_2O_3$.

Wollheim in 1887 deduced a formula for pure chlorophyll, agreeing with Tschirsch's formula for phyllocyanin, $C_{28}H_{47}N_3O_6$.

The following is a comparison of percentage compositions as given by them:—

	Gautier,	Hoppe-Seyler,	and Hansen.
C =	73·97	73·4	68·3
H =	9·8	9·7	10·5
N =	4·15	5·62	5·1
O =	10·33	9·57	16·9
Ash (Phosphates)	1·75	P 1·37	...
	...	Mg 0·34	...

In reference to the percentages of carbon and nitrogen, it is of interest to note that Sachsse, who showed that the members of his green series contained nitrogen while the others had none, is supported by Professor Gilbert, in a communication made at the last British Association meeting in Aberdeen. He pointed out that an increase in the depth of green colour is not associated with a relatively high carbon percentage, but depends directly on the amount of nitrogen present in the plant.

All chemists are agreed that iron cannot be detected in the composition of chlorophyll, though Timiriazeff has again suggested that all the conditions of chlorophyll and its various reactions would be explained by the assumption that iron in the form of an FeOFe_2O_3 compound is present. All that is yet certain is, the necessity of iron for its production.

Certain of the allied or derived colours of the leaf, as for instance carotin ($\text{C}_{18}\text{H}_{24}\text{O}$ of Arnaud), have been selected for observation with more or less satisfactory results; but of the blue, red, and fluid yellow colours of flowers, Flahault says "the most prominent character of the many they share in common is the exceptional readiness with which they are changed and broken down under the greater number of reagents."

A connection between red in leaf and flower is evidenced, according to Professor Schnetzler, by the fact that tannin occurs more plentifully where such colour is present, either in flowers or in young leaves.

Although many botanists regard the fluid colours—red, blue, or yellow—as derivatives of chlorophyll, Vines states that "as yet there is no direct proof that they are derivatives." From the researches of Schimper, mentioned above, it is evident that, in the words of Professor Marshall Ward, we have a "genetic and therefore real relationship" between green and

red solid colours, that is between the chloroplasts and the chromoplasts; as yet, however, we are not certain of a like relationship on the part of the fluid colours.

Hansen assumes that there are four distinct pigments in plants:—Lipochrome-yellow (etioline), soluble yellow, flower-red, and chlorophyll-green, and that chlorophyll is not the source of the other pigments.

The passage of brightly coloured pigments from corpuscles to the condition of that of cell fluid has been clearly demonstrated. The transitions and gradations in colour *observable between green leaves and red bracts or flowers* point to a common origin of the pigments, if not in the chlorophyll, possibly in the etioline; but it is possible, nevertheless, to imagine that a red pigment may be directly produced instead of arising as a transition form out of etioline.

It is necessary to remember that, as asserted by Vines, the fluid colours, allied to the aromatic group of substances, are physiologically waste products.

We shall regard them as definitely related to the chlorophyll colours—chlorophyll itself being produced when the metabolism is constructive; red or other colours when it is destructive. Instances of this we shall deal with when considering colour-changes.

PART II.

Colour-Changes.

Colour-changes may be, perhaps, most suitably considered under the following heads:—

1. Those induced artificially by various reagents; and those induced naturally, by the presence of substances of a like nature in the cells of the living plant.
2. Those associated with particular environments; which environments are either directly or indirectly the cause of change.
3. Those characteristic of definite conditions of growth. (These conditions may or may not be evidently referable to the influence of special environment.)

1. The colours produced from chlorophyll by means of various reagents, either in the cells of the plant or in solutions, have been numerous enough to lead to the assertion that, "given a solution of chlorophyll, it is possible by means of acids and alkalies to produce all the colours exhibited by flowers and fruits."

It does not concern us to know whether such colours are produced by decomposition or (as is probable at times) whether they exist mixed with the chlorophyll in the plant (a question which was alluded to in the first part of this paper), but we may notice in detail various of the ways in which such changes may be brought about.

(A) They may result from mere mechanical separation—for instance, by solvents such as fresh water, borax-water, and alcohol, by which means, among the Florideæ, Fucaceæ, &c., brown and red colours, normally obscuring the chlorophyll present, may be quickly dissolved out. Among the Diatomaceæ, the normal yellow colour due to the presence of phycoxanthine gives place under such agents to green, as this substance is affected more quickly than is the chlorophyll.

(B) That oxidation or reduction may also produce colour-change, we have evidence alike in nature and by experiment. Sorby some time ago asserted that by oxidation yellow changed to red, and red became brown, and if the process be carried further, the coloured substance may totally disappear. Timiriazeff has shown that chlorophyll may be rendered red, and finally colourless, by reduction (with nascent hydrogen), and regain its colour on oxidation. Another example of such induced change to and from green is that afforded by the experiments of Wiesner and Lindt upon *Neottia nidus-avis*. In this plant the transformation of the brown corpuscles to green may be brought about by an increase of temperature by addition of alcohol, or, most rapidly of all, by the action of an aldehyde as a reducing agent.

(C) Very many reagents (iodine-water and chloride of zinc, HCl, &c.) will re-convert yellow corpuscles to green, the colour at times being permanent, at times transitory.

As similar colours appear with widely different reagents, and as the variety of these changes is so great, Russel and

Lapraik were led to judge that the change was of a molecular, not of a chemical nature. Such changes may be observed by any one with the simplest experimenting. I may instance a few of such changes observed last summer by Mr Terras—the isolated instances elsewhere recorded being in no way more instructive.

The commonest transitions were those in accordance with the ordinary litmus-reactions of acid or alkalies; a seeming exception (doubtless due, however, to the action of the acid on the protoplasm of the corpuscle) being where a fixed red changed to a dirty blue with H_2SO_4 and HNO_3 . Fluid-yellows of *Enothera*, *Alyssum*, *Cheiranthus*, were changed to blue by H_2SO_4 , by HNO_3 , by solution of I and KI. The yellow of *Verbascum* failed to give any reactions, whilst many fixed yellows gave those of chlororufin. The yellow of *Linaria* changed to bright red with H_2SO_4 . The red of *Dianthus deltoides* changed to yellow with H_2SO_4 , and as with KHO, this yellow changed back to a transitory red with acids.

From some experiments which I made with a strong solution of KHO, I was able to detect some method among the number of such changes observed by myself and corroborated by many of the instances given by others.

It is known that chlorophyll becomes yellow by the action of alkalies; similarly I found that any other colour might be reduced to the same kind of yellow by the same means. Reds of *Linum*, *Monarda*, and *Dianthus*; blues of *Myosotis*, *Campanula*, and *Salvia*; whites of *Viola*, *Vaccinium*, and *Campanula*, were finally all rendered yellow. The yellow appeared after a longer or a shorter time; but it was remarkable that whilst the whites passed directly to yellow, the blues passed through a transitory emerald-green stage, due of course to the mixing of these colours; the reds became blue, then green, but in the end yellow as the others.

It is apparent that such easily-induced changes need more careful observation and more definiteness of experiment, before even such a transition to yellow as this above noticed can indicate anything to us with certainty. It is essential in all such cases to know as to the strength of the reagent—varying results being given with solutions of different strength in the same space of time.

We may, however, reasonably connect certain well-defined changes which occur naturally, and which are accompanied by the presence of definite substances among the cell-contents, with the naturally present acids or alkalies. The blue, common among the Boragineæ, may thus be explained by the well-known alkaline character of the plant. Similarly, the acid property of vine leaves may have something to do with their rich colouring.

Again, it has been shown that the proportion of various of the substances in the plant may vary at different times—sometimes during a single day. For instance, De Lange has asserted that plants contain a smaller proportion of acids when dead than when alive; that there is an increase of acidity during the morning, and a decrease at night. Similarly, the proportion of tannin (which often is known to produce a red colour in the cells where it is present) varies in different parts and at different times. It is present in many red flowers, and is in greater quantity in young than in old leaves.

Such associated substances may commonly be only produced as results of the same metabolic changes which produce colour; it cannot be denied that they must also influence the colour more or less conspicuously.

2. Passing on to consider those transitions which are due to the direct or indirect effects of environment, it is necessary to notice that this part of the subject has, especially in recent years, received a considerable amount of attention from Continental and English observers, various researches having been made as to the influence of light, heat, moisture, soils, or (comprising all these), as to effects of climatal conditions on vegetation generally, or on colour particularly.

(A) To confine our attention to the first of these, we will consider the effects of light as they are (α) direct, or (β) indirect.

(α) We have before alluded to the importance of light in effecting the change from etiolin to chlorophyll; it is necessary to add that a difference in colour of foliage may be noticed according to the amount of exposure, within certain limits, for instance, where leaves have been less

or more shaded; but it is worthy of attention that this change is not in one direction only. Shaded parts may at times be more green, at times less green, than are parts exposed to more light. Thus strong light has been shown by Pringsheim to be injurious, as it quickly destroys the xanthophyll and the chlorophyll when very intense. Batalin showed in this connection that by very strong light the green colour might be made to disappear from branches of Coniferæ (this without modification of the protoplasmic corpuscle), and that after a few days yellow again appeared in the corpuscles; he was able, indeed, to induce this change in the same branch several times in the course of a summer.

Light appears to affect the production of the fluid colours which Flahault regards as the less stable compounds, such as reds and many yellows. Askenasy and later Flahault point out that this is in opposition to the observation of Sachs, who had doubtless experimented on a very limited number of flowers, and who held that, provided a sufficient supply of nutriment were accessible to the plant, it would colour its flowers as well in complete darkness as in daylight.

As before noticed, the less stable yellow phycoxanthine will disappear in strong light somewhat rapidly; whilst the red, according to Vines, and the yellow, according to Flahault, are found in less proportion in relatively weak light. These colours seem to alter most readily, as indeed we should expect from their suspension in the cell-sap, and they indicate clearly to us that a mean amount of light is most advantageous to their production.

Light appears to effect colour-change in certain green parts of various plants by acting upon the protoplasm which surrounds the chloroplasts, as Sachs has shown, producing a deeper shade when the chloroplasts are aggregated, as they are by day, on cell-walls at right angles to the direction of incidence.

(β) Of indirect effects we have from a longer exposure to light an increase in the reserve material assimilated; this allows of the production of brighter flowers, more material being at the disposal of those processes of metabolism which produce colour. We have also such indirect influences as may be exerted by the production of alkaloids, organic acids,

and ferments mentioned by Vines as resulting in different amount from varying degrees of exposure to light.

Perhaps the clearest example of the chief indirect effect of light, in which a greater amount of assimilated material increases the brilliance of colour, is afforded by the experiment of Flahault upon plants grown at Paris and Upsala; the increase of colour in plants of the same species grown in the latter place is accountable for by the 170 hours more direct sunlight there in the course of the summer.

Cut flowers, which contained chlorophyll, were also shown by Flahault to colour very noticeably when placed in water and exposed to light. He corroborated Sachs' statement for a large number of plants, though not for all, that "flowers" will colour to their normal brilliance in complete darkness, provided they have a sufficient supply of nutritive material, which may be converted into colouring matter. Certain plants depend for much of their brilliancy on assimilation which takes place in leaves of the same year, and therefore they do not colour so brightly if their leaves are withheld from light, or injured so as to prevent perfect assimilation.

(B) The effects of heat in nature are all indirect in a similar way. It affects colour only as it quickens or retards the metabolic processes of growth, as it increases or diminishes the supply of reserve nutritive material in the plant. From this cause may be explained the failure of many flowers to colour brilliantly, or at all, during exceptional or ordinary winters, as has been noticed of the single stock. This will also afford a partial explanation of the asserted prevalence of white and yellow flowers during winter, if such is proved to be really the case. Certainly it is to an impoverished nutrition, largely brought about by change in temperature, that is due the fact of a cold damp winter producing white varieties, or of a droughty summer red varieties. The brilliant red assumed by many Algæ, as, for instance, *Palmella*, *Oscillatoria*, and *Protococcus*, according to Brun, in the shallow waters of alpine lakes, is mainly a consequence of a higher temperature, which prevents further vegetation, and breaks down or changes the green material in the cells into other brightly coloured products.

The more complex condition of heat with considerable

moisture may produce other results than brilliancy of colour, indeed the direct opposite—paleness. This is often shown in the characteristic appearance of “forced” plants, which have, it may be supposed, a rapid extension from quick elaboration of cell-wall, but lack substance, or such stores of reserve material as we have already seen are necessary for colour-production.

(C) M. Sargot, in a paper on “The Influence of Moisture on Vegetation,” tabulates briefly the following results:—“Plants belonging to drier regions when planted in those with warm and humid atmosphere, show a certain amount of blanching; their leaves are pale and thin, with elongated petioles. Their fruits do not become coloured with such lively tints.” The tomato is instanced as colouring in such regions with much less brilliancy than is common in Europe.

(D) Certain of the influences of soils may be better considered when dealing with the effects of increased or diminished nutrition. They have little direct effect, though certain colour-changes are noticeable when some plants are grown in one position or another; as, for instance, is the case with *Raphanus Raphanistrum*, which, commonly having a lilac flower, is invariably yellow when grown by the sea-shore. Or again, Darwin mentions that it was pointed out by a famous grower of chrysanthemums, shortly after they were imported from Japan, that such plants, having a tendency to vary in colour, had, until of more stable character, to be carefully tested in different soils for fear of colour-change resulting.

Although it is probable that an increase in nitrates will deepen the colour of the leaves, yet excess of one material rather than another in the soil, unless absolutely injurious to the plant, will have no effect, because of the selective power of the plant, which takes in general only those substances which are needed.

Where, however, the soil is particularly dry or particularly damp, so as to affect the amount of nutrition, there we have to notice various induced effects upon colouring of leaves and flowers. This is seen in the leaf-colours of *Ranunculus Ficaria*, or of *Arum maculatum*, or in the flower-colours of plants growing near watery places.

(E) Climatal influences resolve themselves mainly into

those of light, heat, moisture, and soils, and accordingly we have to notice differences of colour brought about by these influences in different latitudes and altitudes, or in different habitats of one country or another.

Many papers have been written especially regarding the colour of Arctic plants. Among the more recent of these the researches of Bonnier, agreeing with those of Flahault already mentioned, support the generalisation made by De Candolle, Fries, Schubeler, and others, that as flowers are met with growing nearer the north, the colour of leaves and of the petals may be seen to be more intense. M. Pellas has recorded, from careful observation, that the colour of the same species, grown in the same locality, but at different altitudes, is also increased as higher regions are reached. The colour-change is not, however, nearly so evident as in different latitudes. He mentions that certain plants, as *Silene rupestris*, *Silene inflata*, *Bellidiastrum*, have more rose colour in their petals in higher regions than in lower regions; at the same time, several plants are especially referred to as showing most markedly the colour-change. His facts are all in accordance with the experience of growers of alpine plants, who bewail the lessened brightness of their especial favourites when transplanted to their gardens.

3. Lastly, among the transitions that we may partly account for, must be mentioned those which we may associate characteristically with definite conditions of growth, dependent on the possibilities of nutrition. We have seen, in all the instances of indirectly produced colour-change which have been already mentioned, that the amount of nutrition or the amount of assimilation have been the direct cause of such variation.

Plants, when grown healthily, if exposed to light and heat, take on either green or other colour, and they are not able to produce their normal tint if the assimilation is not normal.

A vigorously vegetating condition is invariably associated with the production of chlorophyll; on the other hand, when plants are grown under unfavourable circumstances, their leaves may show variation in the amount of chlorophyll in proportion to the amount of etiolin, xanthophyll, and other coloured products; whilst, provided there is reserve material

in the tissues of the plant, flower-colouring will proceed normally under such conditions.

It is within the experience of every gardener that coloured foliage plants, such as species of *Coleus*, *Croton*, *Arum*, can be grown most effectively when their roots are "pot bound," or on dry places, that is, with restricted nutrition, not where moisture and a plentiful supply of rich soil will favour vegetation. Many algæ show exactly the same phenomenon. A *Chroolepus*, cultivated by Mr Terras, was invariably green when grown in the more nutritive environment of water, but yellow when out of water. Similarly, van Tieghem mentions that *Bacillus viridis*, though green when in its home of stagnant water, becomes pale in fresh water.

The colour-changes of autumn and of spring occur also when assimilation is at a minimum, when material already in the plant undergoes further elaboration, active vegetation having ceased in the one case and not commenced in the other.

We may recognise a definite order in which colour-changes occur, and Mr Grant Allen has also made us acquainted with a similar order indicating increased specialisation, his arguments being based on distinct morphological specialisations in the plants accompanying the colour.

It is only when we have fully recognised the possible effects of such environments as we have been considering, and the different colour-changes which may be definitely associated with certain conditions, that we are in a position to recognise the possibilities of selection and of heredity in perpetuating such colours as are useful, and in taking advantage possibly of the less, certainly of the most, rapid variations resulting from one or another of the causes that we have enumerated.

Without at present giving any attention to the influence of selection, we may conclude this portion of the subject by enumerating, without special reference to the cause, other natural groups of clearly-defined colour-changes which have been observed in flowers. These have been noticed in individual plants. When they may be distinguished according to the time when they occur, the cause is probably the same in each case.

(a) There are the quick or slow changes as the flowers expand, *e.g.*, in *Pulmonaria*, *Myosotis*, *Orobis*, &c.

(b) There is the (usually slow) change during the life of the plant, completed in one day in certain species, especially those of tropical regions. In such cases the elaboration of coloured product is undoubtedly accelerated by heat or climatal conditions, which may, however, have given a character to the protoplasm which is inherited. In summer too, in temperate regions, when it is not uncommon for flowers to last more than a single day, it is not surprising if colour-change is rapid. Thus, we have such flowers as *Convolvulus minor* and *Hibiscus mutabilis*, which change from white through rose to red in less than twelve hours; so also *Oenothera* and *Gladiolus versicolor*. In two or three days *Lantana*, *Cheiranthus*, *Cobæa*, change similarly—others again still more slowly. Or this change may be partial, as in the spots on the petals of *Arnebia echinoides*.

(c) Then we may distinguish the slow or the more quick change just preceding the death of the flower, as in *Weigelia* and *Cratægus*. This, which is perhaps the most marked colour-change to exhibit itself, is not the change of decay, which is one to brown amorphous masses; it illustrates the regular series of coloured products which under definite conditions are produced from the proteids of the cells. Such a change as that from white to red in *Weigelia* or *Cratægus* well accounts for the origin of the red varieties of these plants.

These colour-changes in single plants show us in the most extreme manner the possibilities of variation when there is but slight difference in the influences at work upon, and the conditions of, the cell-contents. Colour-change, less evidently from the same causes, yet essentially of the same nature, is also seen amongst the different individuals produced from seed in certain species, e.g., species of *Anemone*, *Polygala*, *Anagallis*, &c., especially perhaps among annuals. It is evident that wherever mere conditions of environment do not produce these changes we have to look for a deeper cause in inherited character. It may be that some more subtle character than any we can yet distinguish is imparted to the different ovules of the same parent with its ever-varying protoplasm; and it is essential to remember how great this variation is, for it is shown, not less by flowers changing colour in a single day, than by the occasional pro-

duction (as in *Centaurea Cyanus*, for instance) of two or three distinct colours on different branches from the same root-stock.

In any case, whatever may be the exact difference between the nature imparted to one or another ovule in the same capsule, we have seen sufficient to warrant the assertion that a more or less vigorous assimilation, a stronger or weaker constitution, and even environment directly, do much to influence colour, and this at times to a very marked extent.

When once we may reasonably account for colour-variation in individual seedlings, it is easy to see how, from the continuance of a particular environment, and also by the influence of the important factor selection, particular colours, or colours related to one another in a series, may become prevalent in natural groups, either among the species of a genus, the genera of a natural order, or, further still, among the natural orders of any alliance.

PART III.

Hypotheses accounting for Colour.

Having recognised the various colour-changes that commonly occur under conditions, the general effect of which upon the life-processes of the plant is more or less known, we must now acquaint ourselves with the various hypotheses which have been put forward to account for such phenomena. It is not necessary that we should know as to the exact manner in which vibrations of certain wave-lengths are returned to the eye from the various coloured fluids; this essentially is a question for the physicist.

A colour-change in certain inorganic bodies (therefore called "metachromes"), from red to violet as they contract, and from violet to red as they expand, or as they become more charged electrically with the negative element, was instanced in *Nature* some years ago by a physicist, as possibly throwing light on the phenomena of flower-colour. This was in connection with a paper on "The Seasonal Order of Colours in Flowers," also contributed to *Nature* by Dr Buchan, at that time president of this Society. Dr Buchan observed that of the British plants which flowered between

April and July the average order of the first appearance of the various colours was from blue, yellow, and white to red—the order of the spectrum colours. As at the time attention was called to the fact that light has little or no direct effect upon colour, it was thought that there was only a somewhat remarkable coincidence in these facts; but it may be possible that such data, being corroborated, on comparison with other floras, may indicate to us some indirect effect, following perhaps from the increased or diminished assimilation at one or another time of the year.

A couple of years after the date of publication of Dr Buchan's paper, there appeared, also in *Nature*, an article on "The Origin and Distribution of Organic Colour in Nature," in which, after opening with the statement that "colour throughout the realms of organic nature is a factor hitherto held to be the most capricious in its distribution, and the least amenable to any fixed law," the writer proceeds to show that it occurs in harmony with the "law of polarisation." He points out the prevalence of complementary colours, as in the red eye-speck with the green of *Volvox*, or in *Phæronema*, which is coloured orange, whilst above is the ærurian blue characteristic of the ocean in the abyssal depths which this organism inhabits. It is doubtful whether an explanation in such terms is any more satisfactory to us, than was the old truly metaphysical one which would have us see in colour and form harmony with "the law of beauty and design," framed to delight mankind.

Thanks to Charles Darwin (who, in this particular revived the work of Sprengel), and thanks to Hermann Müller, we now know that flower-colour has its largest use in gratifying the bee, and that it cannot be spoken of as "wasting its sweetness" when there are around it countless insects to benefit by its attractiveness.

Thus a more real use for colour became evident, and natural selection was called in to explain its presence.

Now, allowing what we wish for natural selection, we have yet to ask ourselves, What is the origin of the variations in colour? how have earlier or later variations arisen which might be selected?

Most of those who have definitely dealt with the question of colour,—treating it professedly in a popular manner, as do

Mr Grant Allen and Dr J. E. Taylor in *Colour Sense*, in *Colours of Flowers*, and in *The Origin of Colour in Flowers*,—have too exclusively drawn attention to natural selection, referring only very inadequately to any physiological reasons for its appearance.

Now it is particularly necessary at the present time for us to refer to these physiological causes, but before treating the subject with some detail from this standpoint, it will perhaps be as well to quote from the writings of those who call our attention mainly to the influence of selection, so that we may see what is the effect of this great natural force, to the universal working of which Darwin has pre-eminently drawn our attention.

We have not to consider from the *Origin of Species*, nor from *Animals and Plants under Domestication*, that Darwin held natural selection as accountable alone for most observed variations; indeed, in one passage he speaks of evidence existing as to the presence of internal causes of variation which were not clearly enough evident to him for formulation; but often he uses expressions indicating that he believed variation to be indefinite, produced seemingly spontaneously, occurring as it were by chance. Indeed, it is evident that he often so spoke of chance or unaccountable variation, where nowadays with greater physiological knowledge we see at once the result of definite and easily recognisable life-processes.

That we are thus in a better position than ever before to deal with such variations as those of colour, is due also to the fact that, just as immediately after the publication of the *Origin of Species* biologists gave an almost disproportionate amount of attention to the action of natural selection, so with an opposite swing, as it were, of the pendulum, we are now ready to criticise natural selection and pay more attention to environment and the nature of the organism.

As a witness to the truth of this fact, we have Mr Herbert Spencer's two articles on "Factors in Organic Evolution," recently published.

That attention was disproportionately given to natural selection in the question of flower-colour is not wonderful, when Darwin was able to state in his great work (to what extent correctly we are now more able to judge), that "if

insects had never existed on the face of the earth, our plants would never have been decked with beautiful colours," and "the beauty of fruits serves merely as a guide to birds and beasts, in order that the fruit may be devoured and the manured seeds dispersed." Also, Mr Herbert Spencer, whilst recognising the fact that "incipient floral colour is found among the Cryptogams, and in all young shoots of spring," adds that this "incipient floral colour would tend to fade away were it not intensified by the action of natural selection."

That such a colour would pass away, and that the intensifying is solely the work of selection, is pretty nearly the opinion of most, I believe; but we may fairly ask, Why should such colour tend to fade away? is it not, *à priori*, just as likely, nay probable, that once having originated, it will of itself tend to increase?

But leaving this consideration for the moment, let us try to explain what is the nature of selection in the case of colour.

It is at the present day more than ever demonstrable that certain plants are now so dependent on insects that they cannot live where such are absent, certain individualised flowers having become so adapted to companion insects, that without them they fail to set seed, and in consequence are limited absolutely in their distribution. This being so does not, however, imply that colour in flowers or fruits did not exist in considerable development before insects and fruit-eating animals existed; whilst also it is very evident that many flowers and fruits at present existing have attractive colours which no insect nor animal makes use of, or is able to make use of, as a result following from the selection or altered form of the inflorescence or of the flower, or the greater profusion of nectar, or the like.

In this connection Mr Russel Wallace says, "in flowers colour enables the insect to recognise the species, but no one has ever asserted that insects improve and alter the colour of flowers by their preference for certain varieties of colour irrespective of the honey and pollen produced." We are glad to find so definite a statement as this of Mr Wallace, for it is certain that the conception of a natural selection, as similar exactly, though not the same in degree, as the artificial

selecting of the gardener, is more common than Mr Wallace supposes.

The following extract from Mr Grant Allen's *Colour Sense* illustrates the popular and, to the thoughtless, really misleading manner of treating the subject:—"Insects produce flowers; flowers produce insects. The colour-sense produces a taste for colour; the taste for colour produces brilliant butterflies and brilliant beetles. Birds and mammals produce fruits; fruits produce a taste for colour in birds and mammals. The taste for colour produces the external hues of humming birds, parrots, and monkeys; man's frugivorous ancestry produces in him a similar taste, and that taste produces in him the final result of human chromatic arts."

From this passage there is little information other than that there exists a remarkable interaction between plants and animals. With a similar attitude and manner, Dr J. E. Taylor speaks of "various colours held in reserve, to be brought out at a moment's notice." He instances the three-coloured varieties of *Anemone patens*, regarding the separation of the colours as a clear case in which nature has provided the plant with "three kinds of bait," just as a novice in the art of angling will be advised to provide himself with differently coloured flies.

Mr Wallace says, regarding sexual selection (and the passage is as applicable to the selection of flowers as of mates), "there is not one particle of evidence to show that minute differences in the colour of the same species are observed by insects, still less that such differences are so important to them as to lead to the rejection of a healthy and well-organised mate" (or individual).

Thus selection of flowers is dependent, not on minute variation in colour, but on such changes as we may expect would be appreciable in the size of the flower; in the grouping of several flowers together by shortening of the axis; and on sudden or conspicuous changes in colour, such as might be brought about by several of the factors of the plant's environment to which we have alluded. So in that part of the plant where characteristically there is evidenced a shortening of the axis, where reproduction prevails in contradistinction to vegetation, where also natural selection acts towards the

production of the most individualised flowers, there we may expect the colour to be more intense, but we cannot say that the intensification is entirely the result of natural selection.

But as giving us the first hint of a cause of colour-change, we may refer again to the passage, written twenty-five years ago, by Mr Spencer in his *Principles of Biology*:—"Incipient floral colour existed among the Cryptogams and among all young shoots of spring. . . . Failure of nutrition may be expected in parts the most remote from the roots, the ends of lateral axes are therefore the most probable points of fructification. . . . But if these points at which nutrition is failing are also the points at which the colours inherited from lower types are likely to recur, then we may infer that the organs of fructification will not unfrequently coexist with such colours at the ends of such axes."

Here it will be seen that Mr Spencer accounts for the co-existence of colour and of flowers, but he fails to see the real physiological significance of their correlation. He attributes the appearance of colour at the ends of axes to heredity, not to lack of nutrition. We meet with various re-statements of this assertion of Spencer's by other writers, as, for example, in *Colour Sense*, where this passage occurs:—"We can hardly resist the inference that coloured whorls represent an intensification of the natural tint, such as is to be seen in spring shoots and in autumn leaves." Elsewhere, Mr Grant Allen notices more clearly than did Mr Spencer, as judged by the above extract, that the physiological condition of such highly coloured parts is that "they are expenders, not accumulators, of energy." We may take this statement, or we may take the statement by Vines, "that colouring matters are physiologically waste products," as roughly indicating the position we wish to emphasise, viz., that, in contrast to the green of chlorophyll, "colour" is to be regarded essentially as a product of a destructive metabolism (katabolism) in the cells in which it occurs.

Microscopic examination as to the actual conditions of the colour-containing cells has revealed to us, in the hands of Schimper, that not only does the colouring matter result as a product from the destruction of the protoplasm of the corpuscles, but that "its development, in what are to become chromoplasts, is frequently attended by a disappearance of

the starch grains on, or in, the colourless corpuscle (leukoplasts) or chromoplasts from which the chloroplast arises."

But, in the vast majority of cases, although we may not, as here, have direct evidence of the destructive metabolism of the cell-contents, yet we are fairly entitled to judge from the circumstances of the cell's growth, whether the conditions are those favouring a destructive or a constructive metabolism (anabolism).

If we consider, in the first place, the conditions accompanying the most universal of all vegetable colour-changes, that of autumn; if we associate this colour-change with that of spring (in both these cases the colour appearing not only in trees, but in the smallest herbs, in flowering or flowerless plants); and, finally, if we associate with these two colour phenomena, that of reproduction, we may see at once an identity in the conditions which enable us to bring them all under a homologous explanation.

Colour "among young shoots of spring" is where carbon-assimilation has not yet commenced, but where the growth is at the expense of stores obtained in the previous season; colour in autumn—in the brilliant rosettes of *Sedum* or *Vaccinium*, in *Azalea* or *Acer* (which are as attractive to insects as any flower)—is where assimilation has ceased, and further elaboration or alteration of the cell-contents takes place; colour in the cells specialised for reproduction is also essentially produced where assimilation has given place to an opposite function, by which the young ova grow at the expense of materials elsewhere assimilated by the parent.

To give two excellent examples of this, we may notice the colour of the flowers of *Cupressus Lawsoniana* (seen at our last meeting), or the change of colour in mosses and many alge when reproduction commences.

In regard to the formation of flowers among Phanerogams—if the nutrition be very abundant under conditions favouring carbon-assimilation—green and healthy leaves will be produced, as is in the experience of every gardener, often to the exclusion of flowers.

Professor A. Sachs (who was conducting a series of experiments with the view of determining the cause of flower-production) noticed that when plants were grown in yellow light

there resulted a remarkable predominance of leaves, and a scarcity of flowers; whilst in white light the vegetation was less vigorous, and flowers very abundant. He was led to believe that the production of flowers was therefore favoured by the ultra-violet or invisible rays, which excited some unorganised ferment to take effect at the growing points. We may regard this conception of Professor Sachs as showing that when assimilation or the vegetative power is (practically) *nil*, then, as in the ultra-violet rays, elaboration of flowers or of colouring matters may take place. Whether or not the destruction of the protoplasm necessary to colour is aided by a "principle acting like a ferment," in however small quantities, remains to be seen—it would not alter the conditions, which would be indeed the more characteristically katabolic.

The gradations in form and colour from the assimilating leaves of the stem to the coloured non-assimilating and, at the same time, smaller bracts or leaves of the flower, is remarkably well seen in widely different plants—very clearly in the brilliant inflorescence of *Canna* and in *Epilobium*. Although all will agree that the small size of coloured bracts of the inflorescence is evidence of a checking of vegetation, and of the absence of assimilation in such parts, yet it is perhaps necessary to refer to the comparatively large size of most petals. It is found, however, that though petals are often large, they are formed of the most transitory substance, they are, in fact, so produced that they make a display at as little expense as possible. Undoubtedly if a flower normally $1\frac{1}{4}$ inch become $1\frac{1}{2}$ inch in diameter, we might suppose that such an exuberant growth would be liable to be influenced by the selective power of an insect's discerning eye. But we may call to mind the very large flower of the night-flowering *Cactus*, which is produced when assimilation, and what van Tieghem calls chloro-vaporisation, have ceased, and when the plant is therefore in a condition to pour its surplus elaborated material into its flower-bud. This growth, too, of the most elementary tissue is particularly evanescent, being suited only to last the night.

But not to confine our attention to these three chief conditions of colouring, nor to the correlation between flower-production and colour-production, we may notice that all the

cases of colour-transition to which (in Part II.) I drew attention are capable of an homologous explanation in agreement with the explanation so far given of autumn and spring-colour and that of reproductive axes.

Thus colour appears, or undergoes change, in

(1) Parts farthest from the supply of nutrition, where there is either less material for elaboration, or where more elaboration has been undergone by the coloured substances.

Ex.—This increase in colouring may be seen in single inflorescences even, tips or whole rays of *Compositæ*, in *Silene*, &c. (Pellat); exterior of fruits, as apples; this especially on—

(2) The sunny sides, where the cells are exposed to influences which will quicken or increase the metabolic changes in the cell-contents; also indirectly seen in effects of light, heat, and soils.

Ex.—Exteriors of roots and seeds (turnip root).

(3) Where growth is evidently effected at the expense of stores of material, as in tubers and shoots from perennial root-stocks—*Asparagus*, *Lapageria*.

(4) Lower colours of these series of colour-products are produced in place of higher products, as in albinism, and blanching from weakened constitution, implying a less vigorous vitality, and less material assimilated which will give brilliantly coloured products.

(5) Colour in flowers during their growth when opening, or before death, occurs with greater or less brilliancy as the metabolism is hastened or not.

(6) Colour results directly from various chemical actions artificially or naturally observed, of which cases, that where it is a result of oxidation (reds from yellows, and deeper colours from the reds) affords the clearest evidence of destructive metabolism.

We must, of course, leave it to the chemist or the physicist to decide as to whether the later coloured products are in themselves more complex, or due to a splitting up into simpler substances; or whether, as suggested by Russel and Lapraik, the colour-changes observable in most cases with such different reagents are due to molecular rather than chemical alteration of the substance.

Certain striking correlations also afford us definite hints as to the cause of colour. Of these we may notice those cases in which a change of colour in the flower or fruit (due to some constitutional alteration) is indicated in an altered or similar shade in the colour of the ordinary leaves. This has been seen in black, red, or white fruited vines; in *Pernettya*, in *Erica*, *Cineraria*, *Chrysanthemum*, *Camellia*, and other plants. Darwin mentions several such correlations in *Variation of Animals and Plants under Domestication*; and it must be within the knowledge of all that skilled gardeners will, with remarkable precision, recognise different florists' varieties by the habit of growth, or by minute differences of leaf alone, and this among hundreds of the same genus.

Quite as striking is the correlation of secreting surfaces or honey glands, with more or less brilliancy of colour.

The secreting surface is essentially a more or less localised part of the plant, where not only is there no carbon-assimilation, but a surplus of somewhat altered nutritive material is being given out by the plant. The much coloured and viscid flower-stalk of *Lychnis viscaria* is also something more than the outcome of a happy variation with a deadly stickiness to repel insects, and a brilliant colour to attract them; the colour and the secretion are naturally linked together. So also the colour of honey guides, though perhaps as clearly subject to selection as any part of the plant, has a natural reason thus afforded for its presence, at any rate in its less specialised form.

Similarly, also, we see some reason for the presence of "spots of colour in the more highly modified parts," and for what has been called "compensation" in variation, as in the case of *Dianthus barbatus*, with its crowded, brilliantly coloured, transitory flowers mentioned by Dr Taylor.

It is not possible to mention this subject of the correlation of colour to other products of elaboration without referring to a most interesting passage from an article by Mr Russel Wallace, when offering objections to Mr Grant Allen's treatment of sexual selection. He says that, among certain groups of butterflies, Fritz Müller has discovered that there exists a sexual allurements of a peculiar odour given out by special patches of scales in individuals which are very brilliantly coloured. This fact, he remarks, "is a clear indica-

tion that colour is not a sexual allurements" (we might say, is not to be regarded only as a sexual allurements), "or we should find it most developed, not in conjunction with, but in the absence of, the attractive odour."

Other instances of the correlation of colour to size or vitality among animals as among plants, will suggest themselves to the biologist; for instance, in the male "stickle-back" we recognise true and physiological significance in its indication of an exuberant vitality; for it has, no doubt, some purpose in indicating to the female the exceptional power of a would-be mate, just as in the spring "the freer crimson on the robin's breast" may be supposed to do likewise; but it was not because the female fish or bird liked colour *per se* that this was developed.

It is needless to refer in any detail to the evidence, which is overwhelming, in favour of a regular series of colours indicating progressive development, in such elaboration of further products. From the reactions of colouring matters, from the changes in the life-history of the individual and of the race, it is clear, as pointed out by Mr Grant Allen, that such a series from yellow to white, passing to red and blue, is a natural one. We do not need, however, to recognise that all the coloured whorls of flowers came from yellow stamens, for we have seen that green being the colour of vegetation, with its essential function of carbon-assimilation, yellow is but a stage to this, which may be given to any organ for a longer or shorter time as vegetation is checked; whilst white and red are also produced by its further or continuous checking; no considerations of morphological evolution affect the question.

We have thus a physiological meaning to give not alone for green, and for "colour" as opposed to green, but each colour, rightly considered, may have for each plant a special significance.

Darwin showed that the commonest variation of the Japanese *Chrysanthemum* was the production of yellow; in which doubtless the garden varieties reverted to a simpler colour more nearly like that of the chromoplast of their ancestors, than that resulting from the high art of the Japanese cultivator. Similarly, it would not be difficult to explain, in terms of increased or diminished possibilities

of vegetation, the striking fact mentioned by Darwin of a double yellow hollyhock which, one year, suddenly turned into a pure single white kind, and in which subsequently a branch bearing the original double yellow flowers re-appeared among the other branches.

Or, in conclusion, to take a yet more interesting case, it is recorded by Darwin in the same work,—*Variation under Domestication*,—that “white tubers of potato may be obtained from purple varieties by planting eyes which have so varied. A plant in Lancashire, of Kemp’s potato, which is properly white, produced two tubers which were red. The red kind was propagated in the usual manner, and kept true to its new colour, and, being found a more productive variety, soon became known as “Taylor’s Forty-fold.”

Such examples as these last, and many of the preceding, should enable us to judge with increasing precision, although it may still be with indistinctness, as to the meaning of colour physiologically, not merely its meaning with relation to insects, the only part of the plant-environment to which it has so far been clearly shown to be related.

It will be seen that I have gathered together references to a considerable number of recent pamphlets, of which the main facts are incorporated in my paper; but as the list of papers includes all those which have been reviewed in English science reviews within the last ten years, it is probable that most if not all of importance, of later date than the papers mentioned in Professor Vines’ *Lectures on Physiology*, will be included in the lists. They do not profess to be perfect reference lists to recent literature, they are essentially those from which this paper has been compiled.

In referring to some of this recent literature, it is very far indeed from my wish to undervalue any of those popular works mentioned, which have, in so excellent a manner, delighted a very large number of readers. I can only confess that, from the present standpoint, these works appear to me to have dealt very inadequately with causes of colour-variation, and to have given to the influence of selection by insects, the use of it, a somewhat undue prominence.

The fact that the present paper is an outcome of the one on “Floral Colour,” written by me in conjunction with Mr Geddes, in which the influence of natural selection was

depreciated, must be taken as an indication that the interest and criticism then aroused stimulated me to consider the question afresh and in more detail. This subsequent work has enabled me to see more clearly, in regard to colour, at once the immense power of selection, and the limits to its action. This I have attempted to bring out in this last part of my paper. It would not perhaps be incorrect to assert that next to the fact of evolution comes the fact of natural selection—more than any other realised within the century, to modify all our manners of learning, our thoughts, and our future. Yet, notwithstanding its importance, however we look at it, natural selection is only a selecting; having recognised its potency, we need to push back our inquiry, to find out as to the mystery of variation, as to those causes or tendencies which, when laid hold of by selection, and impressed by environment, have given to us progress and evolution of every advanced type, of even simpler organisms out of every organic structure.

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On the Leaves of Climbing Plants. By W. E.
FOTHERGILL, M.A.

(Read 14th June 1888.)

Some time ago, while working at climbing plants in quite a different connection from the present, I noticed that the leaves of most of the plants I was handling were cordate, sagittate, hastate, and sometime peltate. After drawing up