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THE BRITISH ASSOCIATION AT DUNDEE.

SECTION K.

BOTANY.

OPENING ADDRESS BY PROF. FREDERICK KEEBLE, SC.D., PRESIDENT OF THE SECTION.

IT is with more than the normal trepidation natural to presidents that I, who have worked on the borderlines of several biological sciences, undertake the task of addressing the members of this section. As well might a rogue and snapper-up of unconsidered trifles recite his doggerel songs before a bench of learned magistrates.

Therefore, although I have studied from their works the ways of presidents, and although I shall strive to keep the path which they have mostly trod, yet should I stray I plead with Autolycus that—

> "When I wander here and there,
> I then do most go right."

The addresses which I have consulted show me two alternative models.

I may take all knowledge for my province and discourse on the progress of our science as a whole. This is Ercles's vein, a tyrant's vein. Or as a lover of a department of the science and more condoling, I may confine my address to a special branch of botany. Each method has its merits and its drawbacks, and the one is corrective of the other.

The departmental method depicts the tree of knowledge in sympodial symmetry. The branch which the president of one year holds out for our inspection is seen arising from an erstwhile dormant lateral bud far back from the growing point of the branch exhibited by his predecessor. Under the magic of the presidential hands the new branch grows as grows the enchanted mango. Like the lean kine, it eats up the fat kine, and by the end of the address it dominates all other branches.

The general method shows the tree in other guise. As an artist is wont to paint a tree, so the historian draws it on monopodial lines, with branches standing in due subservience to the leader and in strict coordination with one another. Together these methods tell the truth, which is that the tree of knowledge grows, like many another broad-leaved tree, by a mixed process of monopodial sequences following upon sympodial developments.

What is to the specialist, and indeed for a space is, the luxuriant predominance of his branch appears in historical perspective but as a new lateral for the extension of all the sublateral shoots of science.

Such a new basis for the further growth of all the branches of botany is provided by the lusty shoot of Mendelism, and after weighing the alternatives, and with the reserves announced already, I propose to try to show that this recent outgrowth of the tree of knowledge is destined not to mar its symmetry, but to aid the growth of the whole crown. This, my chief task, should have been my first care had not an event occurred since the last meeting of this Association which compels me, in common with all botanists, to divert thought from its preoccupation and to look back along the route which our science has travelled during the last few decades.

That event, I need not say, is the death of Sir Joseph Hooker, a former president of this Association and twice president of this section. The most venerable and distinguished of British botanists, Sir Joseph Hooker was well-nigh the last survivor of that band of Victorian naturalists who helped to lay the foundations of biology and to disseminate broadcast the knowledge which they made. The story of the labours of that group of naturalists—Lyell, Darwin, the Hookers, Wallace, Huxley, Galton, and others scarcely less distinguished—has been told so often that there is no need to re-tell it now. Nor need I recount the work of Hooker. His discoveries are known and require no re-enumeration. They are incorporated with the common fund of knowledge. British botanists will determine, doubtless, to consecrate a special occasion to the commemoration of Hooker's services to science and to the perpetuation of his memory. My duty it is to express, on behalf of native botanists and of our guests who honour us with their presence, our sense of loss in the death of Sir Joseph Hooker and our admiring recognition of his achievements.

And with the example of that long life devoted until its latest hour to the pursuit of science, I would fain address myself forthwith to my special task; but despite my will I find my thoughts enchained in the contemplation of the life and times of Hooker. Systematist, explorer, critic, writer, administrator, Sir Joseph was first and last a botanist. The versatile Hooker was a specialist.

Thus I find myself turned again to the thoughts which vexed my mind at the outset of this address, urged now to ask outright whether the specialisation of our times has the quality which distinguished that of Hooker and his contemporaries.

This is the uneasy phantom that has been haunting me and luring me to the ramparts when I should be wooing my chosen theme. It haunts me, refusing to be laid. Reason fails to exorcise that ghost. Its uneasy presence lingers near me even though I conjure it with specious argument; urging that these days are days of specialisation *a outrance*: that nowadays both in the art and practice part of life we live by the intensive cultivation of small-holdings; that the fields of science are parcelled out in small allotments. Were I—a simple officer—the sole subject of this visitation I should attribute it to fantasy, and with Horatio cry "Tush!" but beside this poor Bernardo, Marcellus, officer and scholar, has likewise seen it "in the same figure like the King that's dead," and who may refuse to entertain a ghost presenting this—the highest of credentials?

Therefore I offer it again my arguments, insisting that at least among our elders we have specialists as versatile as any of the Victorians. The ghost is not impressed. Instead, it rises to a fuller height, and lays its incorporeal finger on the row of volumes which line the shelves above my head. My obsequious eye follows the direction, and beholds Lyell's "Principles," Darwin's "Voyage," Hooker's "Journal," Huxley's "Essays," Wallace's "Island Life," Galton's "Natural Inheritance," and the other classics from his clients' pens. With the dawn of my comprehension the spectre vanishes, and I am alone, but not in peace. The message left with me appears to translate as follows: The present generation has become expert in intensive cultivation of scientific knowledge, but it has forgotten how to market its produce. In the preoccupation of specialisation it neglects the art of expression. It sinks the artist in the artisan. Each specialist exchanges "separates"—hateful term—with other specialists, but few among us are on speaking terms with the cultured general public curious to know what science is achieving.

The translation into common English of our scientific works is done, like that of foreign classics, too much by hacks and amateurs, and too little by skilled hands. The present generation lets its modesty wrong it; for the science of our day is no less full—nay, many times more full—of interest and wonder than that of fifty years ago.

Still worse: to fail to cultivate the art of expression is to blunt the power of thinking, for the adage "clear thinking means clear writing" stands though the subject and object be transposed.

Such is the nature of the charge which my visitant left with me; and though, as it must have known, my rough translation fails to convey the sober grace of the original, I think that I shall not be alone in pleading guilty to that charge.

Nor perhaps will my fellow-specialists resent an attempt to trace the origin of our lack of literary grace. This defect is in part inevitable and in part remediable. Inevitable because of the increasingly engrossing nature of scientific investigation, because of the relatively small natural gift of expression which nature has vouchsafed to the English race, and because, as science becomes more complex, its followers think more and more in symbols, and those who think in symbols are apt to write in shorthand. The defect is remediable because it is traceable in some measure to the training to which we submit our youth. That training neglects too much the literary side of education.

As it seems to me, there is a fundamental error in our mode of training men of science. The error consists in this: that students who come to English universities are treated in intellectual matters not as youths but as men of mature minds. The professorial potter takes the clay as he finds it, and, no matter what its state, fires it forthwith, and lo! in course of time it is converted into earthenware. Were the assumption on which he acts well-founded, the method might be justified. If our undergraduates were, as we assume they are, well found in general culture, trained already in scientific method, familiar with the language of our fathers, and apt also to read and speak and write some other tongue, then let us take them straightway and bake them in the oven of specialisation.

But I at all events have never met those students, and, outside the ranks of genius—which training toucheth not—I believe they do not exist. The error, as I conceive it, lies in our failure to apply, in drafting schemes of training, the biological law that as society grows older its young men grow younger. Undergraduates call themselves men, not solely from a sense of pride, but also in obedience to tradition. Centuries ago they went up to the university as men of fifteen or sixteen; now they go up as youths of eighteen or nineteen. With respect to moral discipline we are not unforgetful of their youth, but with respect to intellectual education we treat them as though they were grown up. Even the saving second subject has, I am told, been discarded from the final honours course. Let me give an example in illustration of our methods. It is found that a student in his second or third year knows no German, and we advise him to learn it. But in what a way, with our tacit approval, does he set about the task! So that he may tear the meaning from a scientific text as John Ridd clutched the arm of Carver Doone and tore the muscle out of it as the string comes out of an orange!

This barbarism we permit, because we know that it is no barbarism but expediency for a trained workman to take up any tool he needs and to use it as he wills. In the elegant language of modern literature, "and what he thought he'd most require he went and took the same as we."

Yet, unless we hold that mental training is a scholastic fiction and that the teacher's sole business is to supply carefully selected and copious provender for the stuffing of students like Surrey fowls, it must be our care to encourage general as well as special culture in our students.

A further criticism which I have to make upon our university methods will seem to some far-fetched. We are prone to forget that the twin gifts of youth are enthusiasm and idleness. The former we encourage, but the latter, falling within the category of morals, we visit with our displeasure. There is, however, an idleness which is not laziness, but a resting period of the organism tired with the trouble of growing up. I could wish that our English universities understood intellectual liberty as well as German universities understand it. We are apt to mind our sheep too much, and to overrate the virtue of docility.

I would plead for more breadth and less special knowledge, for more licensed freedom, a lesser uniformity, a wider search for gifts, and a slighter regard for specialist attainments. It is never too late for a well-trained mind to master a new subject, but he who neglects the substance of education for the shadow of mere knowledge robs himself of half the pleasure of his work and of every chance of greatness.

In attempting thus to diagnose a complaint which some may think is non-existent, I have laid myself open to attack at every point; yet I have a flickering hope that I may be dealt with after the manner prayed for by an examinee whose paper, which I read, contained the appeal: "Mr. Examiner, please temper justice with mercy, for I am so young in mind." This hope I base upon the facts that modern science has at least taught tolerance, and that I have ever found my botanist colleagues conspicuous for this virtue. They understand that even the most minor among prophets prefers the stake to silence, and their good humour acquiesces in the interchange of rôles whereby the martyrdom which should be his is borne by them in listening to his wrathful words.

Anticipation of toleration so undeserved leads me to regret almost that I ever introduced that ghost at all. For now that it has served my purpose I am free to admit that I might have laid it long ago by other and *tu-quoque* arts.

I, too, might have pointed to those shelves, and at the sight of Mendel's work it would have vanished with a blush. For with all their gracious gifts the Victorians whose just praises I have sung failed to discover that Mendel was alive among them, and showing a way to solve the problems over which they themselves were puzzling.

The merit of the discovery of the greatness of Mendel's work belongs to our generation, and those of us who had no share in it have at least the right to applaud the discoverers and to score the discovery to our side.

So I may conclude the contrast of Victorian with modern naturalists with the reflection: theirs, the higher meed of culture; ours, perhaps, the greater perspicacity.

If, as I am prepared to maintain, the greatest gift which an experimental science may receive is that of a new, serviceable, general method, then to no man are biologists more indebted than to Mendel, for such a method he gave to our science. If, further, this claim can be established, I am absolved from the task of answering the critics of Mendelian doctrine.

Who does not recollect the answer which John Hunter gave to someone—Jenner, perhaps—who wrote to that great experimenter expressing doubt of the validity of an hypothesis? "Don't think—try," was Hunter's fine response.

If it were my purpose to discourse on Mendelian doctrine, it would be my duty to carry on that work—like the early builders of that doctrine—with sword in one hand and trowel in the other, and to try in emulation of the pioneers to take an equal joy in using either implement. But my work concerns the method and facts accomplished by its use, and, as I understand philosophy, the writ of criticism does not run in the domain of accomplished fact. A homely illustration will serve to define my attitude. Here is a new knife, and there an old loaf, the crust of which has turned the edge of other implements. If with this knife I cut that loaf, it is idle to tell me that my knife is blunt. One form of criticism, and one only, is valid in such circumstances, and that is the constructive criticism of offering a better instrument. If I want bread, and Mendel's knife can give it to me, I shall go on cutting, indifferent to the stones of destructive criticism.

My business, therefore, is to meet criticism, not by dialectics, but by confronting it with the facts accomplished by this method and by showing that its use opens new pathways on the borders of the unknown.

Now, if we scrutinise the method of Mendelian research, we may see that there can be no criticism of it.

Give a chemist a complex mixture of many compounds to describe: how does he proceed? The chemist sorts out the ingredients, and submits them severally to analysis. Such, also, is the method of the Mendelian analyst. Give him that complex mixture which is called an individual, and he sorts out the ingredients and submits them to analysis. Ask him how two complex mixtures behave when they are bred together, and he re-defines the question in such terms that it ceases to be enigmatical, and becomes susceptible of solution by experiment.

I am not concerned to claim for the Mendelian method the exclusive possession of these virtues. All I claim is that for the work of making a physiological analysis of individuals, and of thereby establishing a physiological classification of plants and animals, the Mendelian method has proved its value. It effects the service by a simultaneous analysis of germ and soma.

Let it be conceded at the outset that this analysis is made, not by direct but by indirect methods. For so long as the physical nature of living substance remains unknown we can scarcely hope to resolve an individual into its physical components. All that can be done is to make comparative analyses of individuals and to discover how their several components differ from one another.

For our present purpose we may represent the individual by an equation:—Individual $= x + c$; where c represents the sum of a long series of characters of the individual and x an imaginary or real groundwork left after all the Mendelian characters—the sum of which is c—have been removed by analysis from the individual. The Mendelian method is concerned directly with the resolution of c into its components. Indirectly it is concerned also with x; for by the pursuit of the method the full value of c may be determined, and hence that of x may be inferred. This concession made, it is permissible to concentrate our attention on the term c.

Thus the business of the Mendelian is to resolve the complex of characters which is possessed by an individual into its constituent unit characters. As a consequence of this experimental analysis Mendelism is enabled to restate the problem of the behaviour in inheritance of two individuals in these terms:—

The complex of characteristics which distinguishes an individual is the expression of the sum of a long series of characters. As the individual arises from germ cells so each character arises from a germ within the germ cells. Such germs of characters are called factors. When two germ cells unite to form an incipient individual or zygote they bring together the similar factors of a given character—one factor from the one germ cell and the other from the other. As the zygote forms the mature individual, so the paired factors give rise to a character of the individual.

The body characters are the flowers of the factorial seeds implanted in the germ cells.

Some characters are simple and derive from one pair of factors only; others are of an ascending order of complexity and may be traced to the co-operative agency of two, or more than two, pairs of factors. In the case of a complex character the determining factors may be unlike one another or they may be alike. Thus two pairs of different factors are required to produce the character of colour in certain flowers; on the other hand, it is at least probable that certain characters are the outcome of repeated doses of the same factorial stimulant. Further, the individual is a dual thing—a double-barrelled gun. Each barrel is loaded with the factorial charge supplied by one of the two gametes by the union of which its duality is constituted. Conversely and consequently a gamete or germ cell is, in comparison with the individual, of single and not of dual nature. It has one barrel only, and therefore can carry or give effect to one, and only one, of the two factorial charges with which the individual was supplied at the time of its formation.

Our image of the double-barrelled gun serves also to illustrate the several states in which an individual may find itself with respect to its charge of factors of any given simple body character.

Both barrels of the gun may be loaded. An individual in like state possesses two factorial charges and produces gametes, all of which are alike in the possession of one of these factors. Therefore, such an individual, when self-fertilised, or mated with its like, produces gametes which are all alike in this respect, and these gametes, fusing in pairs, give rise to individuals which all possess the character in question. Such individuals are homozygous, they breed true to the character.

Neither barrel may be loaded; and an individual in like state is also homozygous. It breeds true to the absence of the character. If a gamete of the former individual meet with one from the latter individual, the resulting zygote is in like case with that of a double-barrelled gun of which one chamber only is loaded. The zygote is heterozygous for the character. Unlike the homozygotes, which breed true, the heterozygous individual does not breed true to the character in question.

By the application of the foregoing propositions and a little arithmetic, it may be predicted that the offspring of the heterozygote fall into three groups—one homozygous for the character, and another heterozygous, and a third homozygous for the absence of the character—and that, further, these types of individuals occur in the proportion of 1 : 2 : 1. Needless to say, the prediction is susceptible of verification by experimental breeding from the heterozygote. These are Mendelian commonplaces with which I should have hesitated to occupy our time were it not for the fact that I desire to emphasise the epoch-making nature of Mendel's method. The magic wrought by genius is potent because it is simple. The rules of Mendelian method are simple. If it be urged that I have broken my promise and strayed from method to doctrine I would ask which of the simple propositions I have stated may be demurred to by any student of biology?

The supreme importance of Mendel's contribution to science consists in this: that instead of mixing anything with anything "in the gruel thick and slab" of a witches' cauldron, he has taught us to cast the horoscope of Fate by the method of genetical analysis of individual characters. Thus the first part of the Mendelian restatement of the old problem of heredity reads: Investigate one by one the modes of inheritance of the several characters of an individual. Choose for this purpose organisms which are as far as possible alike in all respects except for the character under investigation. Carry the experiment to its conclusion, even to the third or fourth generation. If uncertain results are obtained, ascertain before discarding the method whether the uncertainty may not be due to the interference of other characters not to be suspected *a priori* of exercising an influence upon the expression of the character under investigation.

Who, for example, would suspect a morphological character like thickness of stem of exercising an influence on the time of flowering of a plant? Yet such is the case with the pea (*Pisum sativum*), and there is evidence that when this disturbing influence is removed inheritance of time of flowering follows Mendelian rules.

The second part of the restatement of the problem of genetics may be expressed as follows: Only by the use of individuals of proved constitution with respect to a given character may the effect of external conditions on organisms be determined. The study of variation must be preceded by Mendelian analysis and synthesis. Let me illustrate this theme by an example.

The species, *Primula sinensis*, the Chinese primrose, has given rise to many distinct varieties. Among these varieties are some with white flowers and others with magenta, blue, red, or other coloured flowers. Each of these varieties may be obtained of florists in a pure strain—that is to say, in a strain which breeds true to flower-character. For our immediate purpose we will group these varieties into white and coloured forms.

It has been shown, however, that this apparently natural mode of grouping is inadequate to give a correct idea of the genetic constitutions of these races. It would seem self-evident that the white races differ from the coloured races by the lack of flower-pigment; yet Mendelian analysis demonstrates that there are more subtle differences between the different races. These differences become apparent when true-breeding white and coloured plants are crossed with one another; for it is then discovered that two types of white-flowered plants exist, and it is only by their fruits—their offspring—that ye may know them. Thus if certain white-flowered races are chosen for the experiment, the result of crossing white and colour is a coloured F generation. If certain other white races are used and mated with the coloured form the offspring of the cross all bear white flowers. The different genetical behaviours of these heterozygous first generations give the clue to the difference between the two forms of white used as parents. In the former case—that in which the first (F_1) generation consists of coloured offspring—the second (F_2) generation, raised by self-fertilising F_1 individuals or by crossing them with one another, consists of coloured : white in the proportion of 3 : 1.

Whence we conclude that the white used in this experiment owes its character of whiteness to lack of the pigment-producing factor which is present in the coloured parent race. This conclusion is confirmed by the genetical behaviour of the whites of the F_2 generation. Such extracted whites breed true to flower-character—that is, give rise to white-flowered offspring only. White-flowered races which behave in this manner are termed recessive whites.

In the second case—that in which the F_1 generation consists of white-flowered offspring—the F_2 generation, from selfed or intercrossed F_1 plants, consists of three white : one coloured. The coloured offspring breed true. Of the three whites one breeds true to whiteness and the other two give rise, like the white F_1 generation, to three white : one colour. White races which thus impose their whiteness on the offspring of their union with a coloured race are known as dominant whites. Mendelians account for the genetical behaviour of dominant whites by assuming that they carry the character for colour and also a character for colour-inhibition. This hypothesis, which is novel to biology, is amply justified by genetical results. It propounds a series of questions to the physiologist and biochemist, and in so doing exemplifies the fruitfulness of Mendelism. We shall see immediately whether the biochemist is able to take up this Mendelian challenge and what answer he can give to it.

At present, however, we are concerned to show by an example the necessity of prefacing the study of variation by Mendelian analysis. It was stated just now that the cross, dominant white by colour, results in a white F_1. That statement requires amplification. Grown under normal conditions the F_1 individuals bear pure white flowers; but if grown in somewhat higher temperatures the flowers develop a distinct though pale flush of colour. It is easy to show that the factor for colour is unaffected by the changed conditions, for the flushed F individuals yield offspring of the same kind and in the same proportions as those produced by white F_1 plants.

It is fairly evident that the flushing is produced by the destructive action of heat on the inhibitor. In pre-Mendelian times this response to temperature would have been added without more ado as yet another ornament to dress the window of that old curiosity shop which is stocked with miscellaneous and heterogeneous articles all ticketed with the label "variation."

But in the light of Mendelism we may see in this effect of temperature the result of the casting-vote of circumstance on a heterozygous constitution. We may recall instances—as, for example, those provided by the well-known experiments on the effects of high temperatures on insect larvæ—which seem to show that environmental agencies may single out not only characters but also factors for attack. Thus we may begin to cohere in series the hitherto sundered and scattered phenomena of variation.

It is not yet possible to say how much of variation is to be put down to the interplay of characters, or, rather, to the differential effects of external conditions on characters which tend to balance one another; but this at least may be said—that the old and worn controversy on acquired characters was so much waste of words, because the problem purporting to be discussed had never been defined. Like the half of human quarrels, it was a quarrel about words.

It is stated in the books that the formation of peloric (regular) flowers may be induced by uniform illumination. Was the material used in the research homozygous or heterozygous? Does uniform illumination just prevent the unpaired factor from inducing normal growth? If so, what is the effect on the homozygous normal? These are examples of questions which suggest themselves at every turn, and they will abide the answer of experiment. The time is approaching when it will be possible to test the validity of the hypothesis on which the superhypothesis of natural selection rests apparently secure from verification or disproof.

That hypothesis maintains that everything is in a state of flux; that variation occurs at all times and affects all parts. This may be true of multiple mongrels; of organisms which are heterozygous for many characters. On the other hand, nothing is more surprising than the stability of forms which are pure-bred for a fair number of characters, and it is at all events a suggestion not to be rejected summarily that plants pure bred for a considerable number of characters may exhibit a constancy and stability not usually associated with our ideas of living things.

In any case, it is open to the biologist to provide himself with suitable material wherewith to study the range and scope of variation and to investigate the conditions under which the organism discards old characters and regresses or acquires new ones and progresses. It is open to the Mendelian breeder to standardise creation.

Thus in fulfilling the first part of its task—that of defining the pure-bred—the Mendelian method has provided the material for the fulfilment of the second part—namely, the investigation of the conditions which make for the stability and instability of the organism. I think the time has come when this latter task might be undertaken on a large scale and with good prospects of success.

So far I have played the part of one of those street-corner watchers of the skies who offer a telescope for the inspection of the heavens. I have now to take a turn myself, and by means of the binoculars of Mendelism and physiology survey, not the celestial bodies, but certain new features of a small and narrow terrestrial field which this instrument brings within our ken. My survey has reference to the phenomena of the pigmentation of plants, and is confined to those presented by the anthocyan or sap pigments to which the colours of many flowers are due.

Until recently knowledge of the processes of pigmentation advanced along two main and independent lines. One line of advance—that followed with such brilliant success by Bateson and the Cambridge school, as well as by other students of genetics—has led to a wealth of exact knowledge with respect to the factors and characters which determine coloration. The other line of advance, pursued with no less brilliant results by Chodat and Bach and by Palladin and his associates, has resulted in a great increase of our understanding of the biochemistry of pigmentation.

The merit of being the first to combine the genetical with the biochemical method belongs to Miss Wheldale, to whom, moreover, we owe a good working hypothesis of the nature of the processes involved in pigment-formation. The work of Palladin and ot Chodat and Bach is so well known that I need not review it in any detail. To Palladin we owe in large measure the conception that respiration consists in a sequence of enzyme-like actions, the later of which result in oxidations and are ascribed to oxydases. To the same observer we owe also the suggestion that chromogens play a part in the oxidations set up by oxydases, and that these colourless chromogens may undergo either alternate oxidation and reduction and so take a continuous part in oxydase action, or undergo permanent oxidation and so constitute the pigments of the plant.

Chodat and Bach have given us a serviceable conception of the nature of oxydases. According to the Chodat-Bach hypothesis, oxydases are of dual nature; the complete oxydase consisting of two parts—a peroxydase and an organic peroxide. An oxydase reacts with oxidisable reagents, such as guaiacum, to produce a characteristically coloured product. Hence these reagents may be termed oxydase-reagents. Peroxydases react with oxydase reagents only if there be added, as a substitute for the organic peroxide of the complete oxydase, a source of active oxygen in the form of hydrogen peroxide. Both oxydases and peroxydases occur in the cells of plants, and may be identified in extracts therefrom.

The work of Görtner on the pigments of insects adds confirmation to the view that pigments are the product of the action of oxydase on chromogens. Thus he has shown that the black or brown melanin of the integuments of insects is produced by the action of an oxydase, tyrosinase, on some such product of protein-hydrolysis as tyrosin.

Miss Wheldale's studies have led her to formulate the hypothesis that the anthocyan pigments of plants are the outcome of a series of chemical changes of the following order: Glucosides hydrolysed by emulsin yield chromogens which, acted on by oxydases, give rise to anthocyan pigments. The difficulty in the way of further advance lay in the unsatisfactory nature of the methods for identifying oxydases derived from plant tissues. Hence when we turned our attention to this subject Dr. E. F. Armstrong and I made it our first task to search for means whereby we should be able not only to identify, but also to locate, oxydases and peroxydases in plant-tissues. Clarke had tested already numerous oxydase-reagents and found that certain among them are adapted for microchemical use. As the result of a considerable number of trials of known reagents we have found that α-naphthol and benzidine are each adapted admirably for the purpose of locating oxydases. By means of these reagents we have been able to map out the distribution of oxydase and peroxydase in the flowers and other parts of various plants, and although the work is laborious and the technique as yet imperfect, the results afford strong confirmation of the current hypothesis of the mode of formation of anthocyan pigments. This confirmation, however, was rendered possible only by reason of the fact that we worked with races of plants bred on Mendelian lines, and hence of known genetic constitutions.

Our method of investigation is briefly as follows. The oxydase-reagent is used in weak alcoholic solution, the part of the plant to be tested is incubated in the solution for a suitable time, and if no oxydase action takes place—that is, if no characteristic coloration of the tissues occurs—the material is tested for peroxydase by the addition of hydrogen peroxide. The method may be employed for intact corollas or petals or for sections of plant-tissues.

It is important to mention that the first result of immersing a sap-pigmented tissue in either reagent is the decolorisation of the tissue. For example, a corolla of a coloured-flowered race of *Primula sinensis* loses its colour completely after being immersed for an hour or two in either reagent. The decolorised corolla, which in the case of *P. sinensis* remains colourless, is treated with hydrogen peroxide, with the result that a well-marked peroxydase reaction is obtained. The reaction is confined to the non-chlorophyllous parts of the corolla, and does not occur, except in the epidermal hairs, in the region of the yellow or green eye, the tissues of which contain chlorophyll. Indeed, there is good reason to believe that chlorophyll inhibits oxydase action.

By treating similar flowers with each of our two reagents we find that the action of α-naphthol and benzidine are, in a considerable measure, supplementary one of the other. Thus the lilac-blue α-naphthol reaction is confined, or almost confined, to the veins of the corolla, the brown benzidine reaction is exhibited by the superficial (epidermal) cells and also by the veins. In order to emphasise the facts of distribution we speak of the peroxydases of *P. sinensis* as epidermal peroxydase and bundle oxydase. The former occurs in the epidermis and in the epidermal hairs, the latter in the bundle sheath which accompanies the veins.

Similarly, if sections of a stem of *P. sinensis* be investigated they are found to contain a superficial peroxydase and a deep-seated peroxydase. As the result of investigating the peroxydases, not of any unknown variety taken at hazard, but of the several varieties characterised by constant differences of depth and extent of pigmentation, we have been able to show that the distribution of peroxydase in any one race coincides broadly with the distribution of pigment in the most pigmented races. In other words, in *P. sinensis* the peroxydase framework for pigmentation occurs throughout the species, and the building of the several colour varieties is determined by the activity of the factor for chromogen production. If we conceive of this factor as administered in a series of doses we can form a fair picture of the mode of evolution of the series of varieties characterised by increasing or decreasing amount of pigmentation of their vegetative parts.

On turning to investigate the peroxydases in white-flowered races of *P. sinensis,* we shall expect to find from analogy with the peroxydases of the stem that these agents of pigment-formation are not lacking from the corollas of recessive whites. The application of our reagents shows that this expectation is correct and that those white-flowered races which lack the factor for colour contain epidermal and bundle peroxydase. Hence we conclude that the absence of colour from recessive white flowers is due, not to the absence of peroxydase, but to absence of chromogen. This conclusion is in conformity with that arrived at previously by Mendelian methods; for, as we have noted already, these methods demonstrate that anthocyan pigmentation of the flower of *P. sinensis* depends on the presence of one factor only, and that the absence of pigmentation which is characteristic of recessive whites is due to the absence of that single colour-factor.

The result of our investigation of the peroxydases of dominant white flowers is, on the other hand, quite different from that given by recessive whites. When corollas of dominant white races are treated with α-naphthol or benzidine and subsequently with hydrogen peroxide, they show no sign of peroxydase neither in epidermis nor in bundles. Hence such flowers either lack peroxydase or else they contain a substance which inhibits peroxydase from exercising its oxidising action on our oxydase-indicators.

That oxydases may be inhibited *in vitro* has been demonstrated already by Görtner, who has shown that the addition of certain phenolic compounds—orcin, resorcin, &c., prevents tyrosinase from exercising its characteristic action upon tyrosin.

Assuming that an inhibitor of peroxydase occurs in dominant white flowers, it may be supposed to act either by destroying peroxydase or by setting up conditions under which the activity of peroxydase is arrested. Assuming further that the inhibitor acts in the latter way, it follows that if means of destroying or removing the inhibitor be discovered and employed, the peroxydase released from the inhibitory grip should be free to effect the oxidation of our reagents.

This train of reasoning gave us a point of departure for experiment. Starting from this point Dr. Armstrong and I have found in hydrogen cyanide a means of removing peroxydase-inhibition. Thus if dominant white flowers are immersed in a 0·4 per cent. solution of hydrogen cyanide for twenty-four hours, washed, and treated with either of our reagents together with hydrogen peroxide, pronounced peroxydase reactions are obtained, both in the epidermal and bundle tissues of the corolla. Carbon dioxide in aqueous solution produces a like, albeit a less pronounced effect.

Now, it so happened that we had at our disposal a race of primulas, the flowers of which lend themselves peculiarly well to the purpose of confirming these observations. The race in question is characterised by blue flowers with fairly symmetrically placed paired white patches on each petal. We have reason to believe from the known ancestry of this race that these white patches are produced by a localised inhibitor.

Corollas of these flowers treated with α-naphthol or benzidine become quite colourless. When, however, hydrogen peroxide is added the natural pattern is restored. The parts originally blue are stained lilac-blue or brown, according to the reagent used, and the inhibitory patches stand out as in the intact flower as white areas on the coloured ground.

If instead of submitting the parti-coloured flowers directly to the oxydase reagent they are treated first with hydrogen cyanide, and then treated with the reagent and subsequently with hydrogen peroxide, the inhibition located in the white areas is found to have been removed, and the peroxydase reaction is produced over blue and white areas alike.

Hence the Mendelian hypothesis of the inhibitory nature of dominant whites is confirmed by biochemical methods. Moreover, these methods demonstrate that the inhibitor acts not by destroying but by preventing the action of oxydase upon the chromogen.

There are many other aspects presented by the phenomena of oxydase distribution in *P. sinensis* and other plants which we have investigated. Some I may enumerate, but lack of time must be my excuse for not dealing fully with any of them.

The close proximity in the flower of the superficial and deep oxydases suggests that the latter may cooperate with the former in producing flower-pigments. This possibility entails the hypothesis of a translocation of oxydase from the region in which it is secreted to that in which it acts, and there are not a few facts which are in favour of this view; for example, the lines of deep colour which occur along the veins of many flowers, the frequency with which the walls of cells appear to contain oxydase, the occurrence of oxydase in the mesophyll cells which adjoin the bundle sheath, and the evidence provided by the mutual influence of stock and scion in grafted plants and in graft hybrids. Though these and other subjects must be passed over, I cannot resist giving what appears to me to be the most elegant mode of demonstrating the relation between oxydases and pigmentation which we have as yet observed. The plant which has served for this purpose is the sweet William (*Dianthus barbatus*), and any of the old-fashioned races of this plant common in cottage gardens suffices, provided that it be an ever-sporting race. Such a race is known by the fact that it bears, on one and the same head, flowers of different colours. The race which we have used is very sporting, a single plant bearing in one inflorescence deep magenta, pale magenta, white with limited rose flush, and all but pure white flowers.

If a petal of each of these flowers be treated with the benzidine reagent, it is found that the extent and amount of the oxydase reaction, as measured by the distribution and depth of brown coloration indicative of oxydase, coincide precisely with the extent and amount of pigmentation. The full-coloured petal gives a uniform deep brown reaction, the light magenta a uniform but paler reaction, the petal with a limited rosy flush gives a slight reaction, limited to the pigmented area, and the all-but-white petal gives none but the slightest reaction, and that only in the part of the petal which contained traces of pigment. Thus—unless the results are due to a partial inhibition which has eluded our attempts at demonstration—it would seem established that the ever-sporting habit is due to differences in the amount of oxydase in the diversely coloured flowers.

The sweet William is also noteworthy in that it contains white races, some of which give an oxydase reaction in their petals, and some of which give no oxydase reaction. Breeding experiments now in progress will decide whether or no these white races, like those of sweet peas investigated by Bateson and Punnett, mated together yield coloured progeny. If so, the factors for colour, long wandering yet not lost, which meet again in reversionary coloured cross-breeds, may prove to be a chromogen factor and an oxydase factor.

Finally, a brief reference must be made to our observations on the periodic fluctuation of oxydase in plants. Various observers have noticed that plant tissues give the peroxydase reaction much more generally than the oxydase reaction. The observations now to be described indicate that this is due to the greater stability of peroxydase as compared with the organic peroxide.

In certain circumstances a tissue which gives only the peroxydase reaction may exhibit the direct oxydase reaction. Moreover, the extent of the peroxydase reaction, as judged by the depth of coloration of the reagent, varies in similar plants at different times.

Inquiry into the meaning of these fluctuations led us to the discovery that the nature and amount of oxydase contained in a plant tissue varies in an orderly manner according to external conditions.

Among the conditions which determine this fluctuation are light and darkness. Plants subjected to normal illumination possess less oxydase than those which are kept in darkness. After one or two days' exposure to darkness plants of *P. sinensis* contain more peroxydase than sister plants kept under normal conditions of illumination. Moreover, after such an exposure to darkness tissues which under normal conditions give only peroxydase-reactions yield distinct oxydase-reactions.

Whether these phenomena are general among plants we are not yet in a position to say; but repeated experiment enables us to vouch for them in the case of *P. sinensis*. Should the results of similar investigations with other plants show that this diurnal variation of the oxydase-content of plant tissues is of general occurrence, we may perhaps discover therein the means whereby many of the phenomena of periodicity exhibited by plants are maintained and regulated. We know that the light and darkness of the day and night set up rhythms in the plant; for example, that the leaves of various plants assume nocturnal and diurnal positions. We know further that the rhythm thus established may be maintained for a certain time under uniform conditions of illumination. This is the case with the sensitive plant and many another.

Animals also exhibit a like periodicity. Thus some years ago Dr. Gamble and I showed that certain shrimp-like animals, *Hippolyte varians,* roll up their brilliant chromatophores at night and assume a sky-blue colour. When daylight comes they put on their daytime dress by spreading out the pigment of their chromatophores in far-reaching superficial networks. Kept in the dark, these animals retain for many days this periodic habit, and when the hour of night arrives, although they have no light to tell it by, they lay aside their daily garb and put on the uniform of night. So also the plant-animal *Convoluta roscoffensis,* which lives on the seashore, orders its behaviour by the sun and moon. It lies on the sand till the waves of the making tide are upon it, and then descends to security and darkness. When the tide recedes it rises to the light. Even the uncongenial surroundings of a teacup and a laboratory fail to break this habit; for in these surroundings its uprisings and down-lyings keep time with the tides.

To one who has scrutinised with perplexed mind these mysteries of biology, the speculation may be permitted that light and darkness may work these wonders through the control of chemical agents such as oxydases. But though it be legitimate to make a speculation of this kind, it is idle to hunt the unknown to the death without the lethal weapon of experiment, and so I leave it for the present unpursued, and with it my address. We have it on the authority of a poet and philosopher that to the traveller on a lonely road each bush becomes a bear, and I am not oblivious of the fact that oxydases have obtruded themselves with a certain obstinacy in the course of my address. Nevertheless, obsession has its uses and significance, for it is the after-effect of enthusiasm; and though I have dealt, perhaps at undue length, with special problems and with suggestions, I venture to think that I have made out my case for the opportuneness of an *entente cordiale* between physiology and Mendelism.

UNIVERSITY AND EDUCATIONAL INTELLIGENCE.

CAMBRIDGE.—The Henry Sidgwick memorial lecture at Newnham College will be given by Prof. Ward in the College Hall on Saturday, November 9, at 5 p.m., and will be open to all. The subject will be "Heredity and Memory."

The prize of 50l. out of the Gordon Wigan Fund for a research in chemistry has been awarded to D. H. Peacock, of Trinity College, for investigations on "Hydroxyhydrindenehydrazine and its Resolution," "1:2:4-Triketopentamethylene," and "The Theory of Molecular Volumes."

The next combined examination for fifty-seven entrance scholarships and a large number of exhibitions, at Pembroke, Gonville and Caius, Jesus, Christ's, St. John's, and Emmanuel Colleges, will be held on Tuesday, December 3, and following days. Mathematics, classics, natural sciences, and history will be the subjects of examination at all the above-mentioned colleges. A candidate for a scholarship or exhibition at any of the six colleges must not be more than nineteen years of age on October 1, 1912. Forms of application for admission to the examination at the respective colleges may be obtained as follows:—Pembroke College, The Master; Gonville and Caius College, the Master; Jesus College, A. Gray; Christ's College, the Master; St. John's College, the Master; Emmanuel College, the Master; from any of whom further information respecting the scholarships and other matters connected with the several colleges may be obtained. The forms of application must be sent in on or before Saturday, November 23.

Colonel Harding, of Madingley Hall, has offered to the Vice-Chancellor to hand over to the University a sum which will produce an annual income of between 50l. and 60l. a year, to be devoted to the payment of a lectureship in zoology.

A SERIES of ten free public lectures upon natural history, folk-lore, and related subjects will be given in the new Lecture Hall of the Horniman Museum, Forest Hill, S.E., at 3.30 o'clock on Saturday afternoons, commencing October 12.

IT is stated in *Science* that at the September meeting of the Yale Corporation it was announced that since the last meeting three wills have been filed for probate from which Yale University will probably receive during the year about 150,000l. These bequests include 50,000l., unrestricted, by bequest of Mr. Matthew C. D. Borden, and the McPherson fund of between 80,000l. and 100,000l., "to be employed in assisting worthy indigent students."

A COPY of the second issue of the "Register of Old Students of the Royal College of Science, London," compiled by the Old Students' Association, has been received. An excellently reproduced photograph of Sir William Crookes, O.M., F.R.S., the president of the association, serves as a frontispiece to the register. The names of 876 old students are given; of these 729 are associates of the college, and in their cases the subjects in which they took their diplomas are enumerated. Copies of the register may be obtained, price 1s. net, from Messrs. Lamley and Co., Exhibition Road, South Kensington.

THE Secretary of State for India in Council has made the following appointments to the Indian Educational Service:—Dr. W. N. F. Woodland to be professor of zoology at the Muir Central College, Allahabad; Dr. A. N. Meldrum to be professor of physics and chemistry at the Institute of Science, Ahmedabad; Mr. W. S. Rowlands to be professor of philosophy at the Government College, Jubbulpore; Mr. G. H. Luce to be professor of English at the Government College, Rangoon; and Mr. C. S. Gibson to be additional professor of chemistry at his Highness the Maharaja's College, Trivandrum, in the Travancore State Service.

AT the University of Leeds on October 3 honorary degrees were conferred upon Mr. Arthur Cooper, president of the Iron and Steel Institute; Sir Robert Hadfield, F.R.S., a past president of the institute; M. Adolphe Greiner, of Liége; Herr Friedrich Springorum and Mr. J. E. Stead, F.R.S., members of the council of the institute; Mr. Corbet Woodall, Mr. Charles Carpenter, and Mr. Thomas Newbigging, for their services to science in the gas industry; and Sir Swire Smith, Mrs. R. W. Eddison, Mr. W. E. Garforth, and the Rev. W. H. Keeling, headmaster of Bradford Grammar School, for their services to science and education in Yorkshire.

THE students of forestry in Edinburgh University, as part of their practical training, have during August and September been camping out at the Drumbuick Wood, Methven, Perthshire, and part of the Logiealmond estate of the Earl of Mansfield, so as to have the opportunity of measuring timber. The trees were principally Scots pine, larch, and spruce, and these were numbered and measured. The accessible trees were dealt with in detail in 10-ft. sections, while