

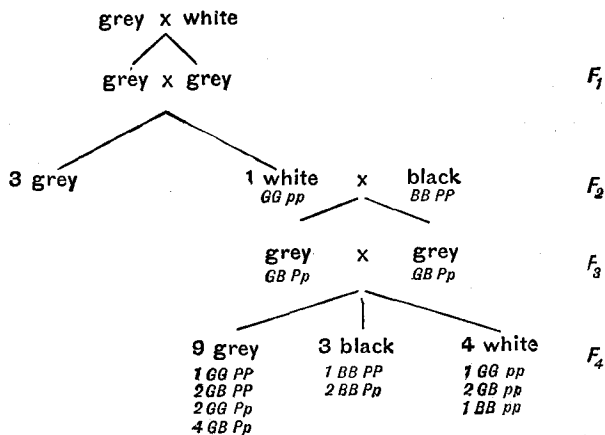
CHAPTER VI

MENDELIAN HEREDITY (*Continued*)

The Inheritance of Colour

IN the simple Mendelian cases discussed in the last chapter the separate allelomorphic pairs were described as wholly independent of one another, and in the manner of their inheritance this description is correct for allelomorphic pairs in general except in special cases, of which examples will be given later. But although allelomorphs of distinct pairs are inherited independently, yet not infrequently they may react upon one another so as to give an apparently combined effect in the individual bearing them. This is especially, but by no means exclusively, seen in the colour-characters of animals and plants. In the list of examples of Mendelian characters it was mentioned that coloured coat in animals or coloured flowers in plants behave as an alternative to whiteness (albinism, i.e. the absence of pigment). But further analysis shows that the appearance of colour depends upon the presence of at least two

factors, in the absence of either of which no colour is produced. An actual example will make this clearer. A white rat is mated with a wild (brown or 'grey') rat, and since colour dominates over its absence the F_1 heterozygotes are all grey, like wild rats. These grey heterozygotes mated together give



coloured and albino in the ratio of three to one. If now one of these extracted albinos is mated with a black rat, the offspring may not be black but *grey*, and such grey individuals paired together will give young in the ratio of 9 grey, 3 black, 4 white.

The explanation is as follows. For the production of colour, two factors must be present, one for the

production of pigment in general (P) and the other for the determination of the actual colour of that pigment (G = grey, B = black). Neither G nor B can produce any visible effect in the absence of P ; a rat without P (represented by p) is thus an albino. The extracted albinos in F_2 from the cross wild grey \times albino then contain G derived from their wild grandparent. These mated with black give *grey* offspring because grey is dominant¹ over black, and the black individual introduces the factor P which was absent in the albino. These grey rats (generation F_3 in the diagram) are thus heterozygous in the pair of factors grey and black (G and B) and in the factors presence and absence of P (P and p). They will thus produce gametes GP , Gp , BP , Bp , which in meeting at random will give 9 zygotes containing G and P , 3 containing B and P , 3 containing G and p , 1 containing B and p . But the combinations Gp and Bp , not having P , are albinos, and so we get 9 greys, 3 blacks, 4 whites.

If in the example just given nothing were known of the origin of the white rat which was crossed with the black (in the generation marked F_2), it would be said that a white variety crossed with a black had

¹ This explanation has been simplified by the omission of the fact that G and B do not represent factors for separate pigments, but that G consists in the addition of a pigment to hairs already containing B . A character dominant in this way is called 'epistatic,' see below p. 75.

produced 'reversion on crossing' and the young had reverted to the ancestral wild form. It is not of course necessary that the albino used to produce such a 'reversion' should itself be the offspring of a grey; such grey-bearing albinos may be bred together for an indefinite number of generations, and still carry the factor G ; or if they were originally derived from a black stock they would bear the factor B . When such stocks are crossed together heterozygous GB albinos are produced, and G and B segregate from one another in the albino just as in the coloured rats in which the colour-factor P is present. *The fact that colour in animals and plants depends on the concurrent action of distinct factors thus explains the phenomena of 'reversion on crossing' which have so long been a puzzle to biologists.*

Among the varieties of the brown (grey) rat only two colour types occur, grey (wild-colour) and black, but in the rabbit, mouse and other animals more are found. In the mouse there are four fundamental colour-types, yellow, grey, black and chocolate. The behaviour of yellow is complicated and not yet thoroughly understood, but of the others, grey crossed with either black or chocolate gives grey; black with chocolate gives black, and chocolate can only appear in the absence of all the others. This was formerly described by saying that grey was dominant over black and chocolate, and black over chocolate, but

this is inconsistent with the hypothesis that allelomorphs exist always in pairs, one possessing a factor lacking in the other. More correctly, then, each colour is allelomorphic with its absence, but the presence of a higher member of the series obscures or prevents the development of the lower. This is expressed by saying that grey is 'epistatic' over black and chocolate, and black over chocolate. Since chocolate is the lowest member of the series, it has been suggested that its factor is indeed the pigment factor represented in the case of the rats described above by the symbol *P*, and that in other colours the special factors are present in addition. In grey mice yellow, black and chocolate pigments are all present in the hairs, but the factor for 'grey-ness' causes the yellow to be restricted to certain parts of the hair. In black mice both black and chocolate pigments are present, but the black obscures the chocolate, and in chocolate mice this pigment alone is present.

The object of this rather special digression is to show how the hypothesis of a series of colour-factors acting together can completely coordinate the phenomena of colour-inheritance, which very few years ago seemed hopelessly confused and subject to no definite rules. It is now possible to forecast with accuracy the results of a pairing between individuals of different colours, if the constitution of the parents with respect

to the colour-factors carried by them is known. Some of these cases have been exceedingly difficult to elucidate because it is often impossible by inspection to determine the constitution of a given individual. This must be tested by suitable matings with individuals of colour lower in the series, and it is then found that the results observed agree closely with expectation.

A more surprising instance of 'reversion on crossing' was discovered by Bateson in sweet-peas. He found that within the white variety known as 'Emily Henderson' two distinct types exist, indistinguishable in appearance, which when crossed together give a purple closely resembling the wild sweet-pea of Southern Europe. The purple reversionary form in the first cross, (F_1), self-fertilised, gives in the next generation, (F_2), 9 coloured to 7 whites. The explanation is that some plants of the white form lack one colour factor (called by Bateson 'C'); others lack the complementary factor 'R,' which if present with C, would produce red pigment. Since colour can only appear when both C and R are present, each parental form is white, but when crossed together C and R are combined in one plant and coloured flowers result. The allelomorphic pairs are C and its absence (c), and R and its absence (r); the purple heterozygote is thus $CcRr$, and produces four kinds of gametes CR , Cr , cR , cr . These mating at

random give offspring in the ratio of 9 with *C* and *R*, 3 with *c* and *R*, 3 with *C* and *r*, 1 with *c* and *r*. But only those containing both *C* and *R* can produce colour and therefore 9 coloured appear to 7 white. Further, among the coloured individuals of F_2 , both purple and red appear, because the factors *C* and *R* together produce only red; to get purple a third factor for blue (*B*) must also be present, which can only take effect in the presence of both *C* and *R*. Since *B* was introduced by one only of the original whites, the F_1 purples were heterozygous for blue as well as for *C* and *R* (with fully represented constitution *CcRrBb*) and hence among the F_2 plants one quarter contain no *B* and in the presence of *C* and *R* are red¹.

¹ In this account, the production of colour (red) is described as being due to two factors (*C* and *R*). The recent work of Miss Wheldale [42] on the chemical nature of flower-colours indicates that the essential bodies are an organic base or 'chromogen' and an oxidising ferment. The work of Chodat and Bach, however, indicates that such oxidising ferments must contain two components, neither of which alone is able to oxidise the chromogen and produce the coloured derivative—anthocyanin. Both kinds of white sweet-pea contain the chromogen, but it seems probable that one component of the oxidising ferment is present only in one, and the other component only in the other. Hence no colour can be produced in either. But on mating the two whites together, the mechanism for the oxidation of the chromogen is again complete, and red colour (anthocyanin) is formed. The purple colour (represented by the additional 'factor' *B*) is due to a further stage of the oxidation of the chromogen than when only red is produced. In some white

In the account given above of the colour-factors in the sweet-pea it has been shown that at least two separate elements are required to produce colour (in this case red), and a third if blue is to be present in addition. But for the production of the various shades or distribution of colour further factors are known, e.g. for the intensification or dilution of colour, and for making the wing-petals of the same or different colour from the standard. Similar phenomena are concerned with colour in animals, of which domestic varieties of the rat provide a simple instance. Rats, other than albinos, are in general either 'self-coloured,' with little or no white (this, if present, is confined to the ventral surface), or 'hooded,' i.e. white with

flowers (snapdragon) experiment shows that the chromogen itself may be absent.

As the purple colour in sweet-peas is due to more complete oxidation of a chromogen than red, so in animals colour-physiologists find that the series yellow, brown, black, may represent successive oxidation-stages of the same chromogen by the same ferment. The various colours of mice, for instance, are not therefore to be regarded as necessarily produced by different ferments, but the inherited 'colour-factors' determine to what stage the oxidation of the chromogen shall be carried. Some confusion has arisen from the assumption that the 'factors' postulated by students of heredity are actual specific colour-ferments, while they may be rather determinants which cause the oxidation of the chromogen to proceed to a particular stage, and may be compared with the factors which determine the production of a rose-comb or single-comb in fowls.

coloured head and shoulders and a coloured stripe along the spine. The self and hooded factors are an allelomorphic pair independent of colour, so that a hooded rat may be black or grey. The factors may also be borne by albinos, and when very young an albino bearing the factor for the hood may be distinguished by the different texture of the hair on the head and shoulders, giving the appearance of a water-mark or 'ghost-hood.' The heterozygote between self-coloured and hooded patterns differs from either parent, being black above and white below—the so-called 'Irish' type of the fancy. Such 'Irish' rats bred together always give both self-coloured and hooded rats in addition to Irish among their progeny. A similar case in rabbits is that of the well-known Dutch marking, which seems to correspond with the hooded condition in rats. In flowers the number of such characters determining the nature and distribution of colour may be considerable, so that among the offspring of a cross between two varieties of Chinese primulas or snapdragons a very large colour-series may be produced, which on first inspection may seem a continuous series from the darkest to the palest; but careful analysis of these cases has shown that the different factors may be recognised and isolated, and the series of colours falls strictly within the rules of Mendelian inheritance when each factor is considered alone.

Hitherto in discussing the interaction of distinct pairs of factors (allelomorphs), colour alone has been considered, but cases are known where colour and a structural character are interdependent in the same way. Interesting examples of this are known in stocks and primulas. When a certain smooth-leaved cream-flowered stock is crossed with a smooth white, the F_1 plants are *purple* and *hoary*, i.e. they revert to the ancestral wild purple and hoary-leaved stock. The purple colour appears for the same reason that the two forms of white sweet-pea gave purple; one colour-factor is introduced by the white parent and its complement by the cream¹. But the hoariness appears because the parents contain a factor for hoariness, which can only take effect *in plants with purple flowers*. The parents are therefore smooth although they contain the hoary factor. When the F_1 hoary purples are crossed together, the F_2 generation consists of purple, white and cream-flowered plants in the expected proportions, but only the purples are hoary. Smooth-leaved purple strains do exist, but these are plants lacking the hoary factor altogether; if it were present, it would appear whenever the flowers contain purple sap.

¹ The cream-colour is due to a quite distinct factor, and the pigment is in special bodies (plastids) in the cells of the petals. The purple colour is due to a pigment dissolved in the sap, and is independent of the cream plastid-colour.

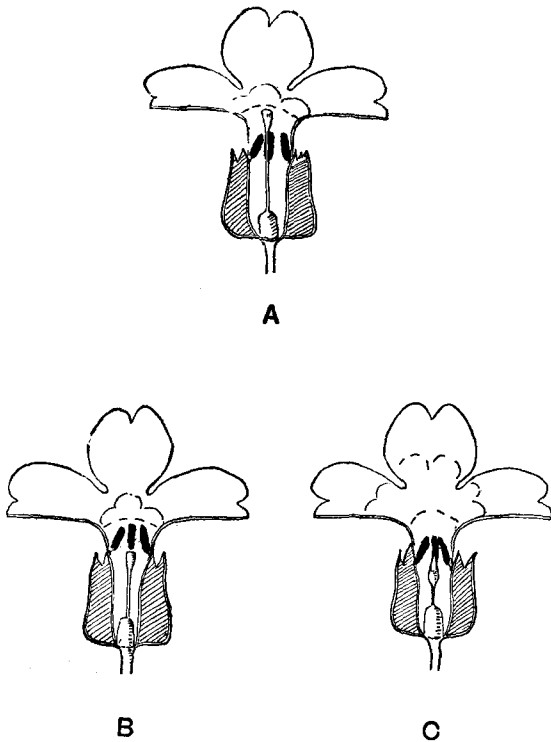


Fig. 10. Sections of Chinese Primula Flowers.

- A. Long-style ('pin-eye').
- B. Short-style ('thrum-eye').
- C. Homostyle.

In Chinese Primulas a curious case of inter-relation between flower-colour and structure has been investigated by Bateson and Gregory. They find that the long-styled and short-styled types of flowers, so well known from Darwin's work, are an allelomorphic pair, short-styled being dominant. But when the long-styled factor is associated with a condition in which the yellow eye of the flower is enlarged to cover about half the area of the petals, the style remains short, although the anthers occupy the typical long-styled position in the tube of the flower. This condition is called 'homostyle' (fig. 10 C, p. 81). When a short-styled small-eyed plant is crossed with homostyle large-eyed, all the (F_1) offspring are short-styled and small-eyed, these characters being dominant. But in the second generation, (F_2), obtained by breeding together these F_1 plants, the following types appear:—

- 9 short-style with small eye,
- 3 short-style with large eye,
- 3 *long-style* with small eye,
- 1 homostyle with large eye.

The long-styled form has appeared in F_2 from short-style \times homostyle, because homostyle is a condition of long-style modified by association with the large eye. When this association is broken, the long-style appears.

From these examples of the interaction of distinct

allelomorphic pairs, many more of which are now known, it will be seen that many of the 'exceptions' to the Mendelian rule which have been recorded may

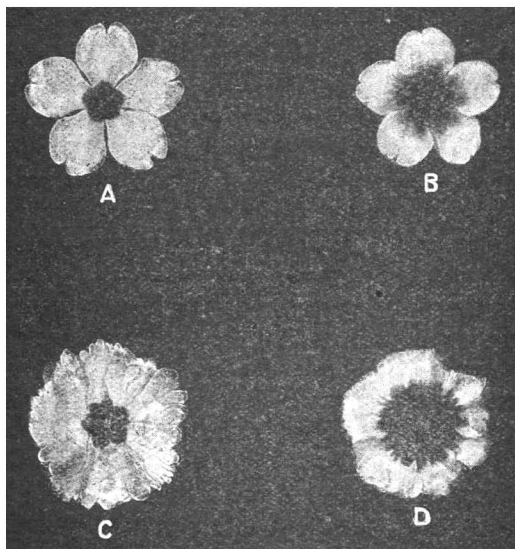


Fig. 11. Some of the types of flowers in generation F_2 from the cross short-style (thrum) small eye \times homostyle large eye.

A. Long-style, small eye. B. Homostyle, large eye. C. Short-style, small eye. D. Short-style, large eye.

In A and B the flowers are of the 'star' type. This character is inherited independently of the style and 'eye' characters. (From Bateson.)

be explicable on the assumption that what appears to be a simple character is really dependent on two or more distinct factors, which become separated on crossing with a different form.

In conclusion, it must be mentioned that a number of cases are now known in which a pair of Mendelian characters are closely associated with Sex. In some cases the sex of the individual determines whether a character is dominant or recessive ; for example, if a horned race of sheep is crossed with a hornless, the male offspring are horned and the females hornless ; and in cats, it appears that yellow crossed with black gives yellow males but tortoiseshell females. In other cases certain Mendelian characters can be borne only by germ-cells which will give rise to one or the other sex. These two apparently different relations between sex and a body character may sometimes be combined ; for example in man, colour-blindness is dominant in males but recessive in females, but at the same time an affected man transmits the 'factor' for colour-blindness only to his daughters, so that while his sons and their descendants are free, his grandsons through his daughters may be affected. Lack of space forbids a full discussion of these phenomena, but they suggest that maleness and femaleness are possibly in reality a pair of Mendelian characters, inherited in the manner described in the last two chapters.