CHAPTER IV

COMMON MODES OF INHERITANCE

"Lord, I find the genealogy of my Saviour strangely checkered with four remarkable changes in four immediate generations.

1. Roboam begat Abia; that is, a bad father begat a bad son.
2. Abia begat Asa; that is, a bad father a good son.
3. Asa begat Josaphat; that is, a good father a good son.
4. Josaphat begat Joram; that is, a good father a bad son.

I see, Lord, from hence, that my father's piety cannot be entailed; that is bad news for me. But I see also, that actual impiety is not always hereditary; that is good news for my son."—THOMAS FULLER, *Scripture Observations*, No. viii.

ESPECIALLY among the lower animals, the offspring sometimes appear to us as if they were perfect reproductions of the parents, and we venture to speak of complete hereditary resemblance. Thus, in a crowd of Myriapods collected from one place at the same time, no individual peculiarities could be detected. A daughter-Hydra may be easily obtained which seems identical with the parent. A series of generations of green-flies or Aphides may be studied and no individual peculiarities discovered.

In other words, there seem to be cases in which generation succeeds generation without any variation.

But there is every reason to suspect that in most cases the apparent absence of variation is illusory, and due to a lack of sufficiently intimate acquaintance with the individual organisms. The sheep which seem "all the same" to the careless eye are often known individually by the shepherd, and it is easy to demonstrate that the peas in one pod are often far from being alike. Similarly, the members of a group of individuals may seem "all the same" even to the naturalist's eye, but minute differences are soon detected by the expert who has devoted years to becoming intimately acquainted with that particular type. There are observable differences between sister-bees or ants, between the rooks from one clutch or the pigs from one litter. Even when there is only one parent—*e.g.* a self-fertilising liver-fluke or a parthenogenetic water-flea—there may be variations among the descendants. There is no doubt, however, that the range of variability differs greatly in different types, and it is obviously in cases where individual peculiarities are frequent and well marked that we can most hopefully study the relations of resemblance and difference between parents and offspring, or between the members of a series of generations. In horses and dogs, in sheep and cattle, in rats and mice, in rabbits and guinea-pigs, in pigeons and fowls, in butterflies and small, rapidly breeding crustaceans, in wheat and barley and maize, in peas and stocks, and in man himself, there is ample opportunity for studying *the modes of inheritance.*

§ 1. *Though Prediction in Individual Cases is insecure, there are some Common Modes of Inheritance*

When we are dealing with the generations of an animal or plant in regard to which previous observation has shown us that the members of the species are strikingly uniform in their characters, we may venture with some security to predict that

the offspring of a pair will as usual exhibit more or less complete hereditary resemblance to their parents and ancestors. And yet this prediction may be falsified, for variations may suddenly crop up without known cause.

Similarly, when we are dealing with the generations of a so-called "pure-bred" race of animals or plants, we may venture with some security to predict that the offspring of a pair will exhibit, as regards their more essential features, a large measure of complete hereditary resemblance to their parents and ancestors. And yet in individual cases this prediction also may be falsified; for no known reason a "freak" or "sport" may unexpectedly appear.

When we consider the variable nutritive conditions of the germ-cells, the subtle processes of maturation and fertilisation, and the intricate nature of the environment appropriate to each development, we cannot be surprised that the result may often belie individual prediction. The possibly anecdotal instance, cited by Lucas, of the twin children of an Antillean negress—one white with long hair, the other black with woolly hair—may serve as a diagrammatic illustration.

On the other hand, experience shows that, in spite of uncertainty in regard to individual cases, there is often perfect certainty as to the average results where we have to do with large numbers; that the degree of resemblance to parents and ancestors is sometimes capable of precise prediction; that in particular sets of cases (Mendelian phenomena, see Chapter X.) we can definitely predict how many of the offspring will be like the parents, how many like one grandparent, how many like another; and that, apart from such statistical generalisations, there are what we may call *alternatives of expectation* with varying degrees of probability. In other words, *there are certain more or less well-defined modes of hereditary resemblance which occur very frequently*. To explain and illustrate three of these is the object of this chapter.

A discussion of the different modes of hereditary resemblance is somewhat hampered by an exuberant terminology, and by the fact that different authors have sometimes used the same term in different ways. We read of inheritance being unilateral and bilateral, unisexual and bisexual, blended and conspired, neutralised and combined, direct and collateral, atavistic and progressive, and so on. We have tried to reduce this complex terminology to a minimum. This is the more justifiable since we cannot doubt that all the ordinary phenomena are of a piece, that many of the ordinary modes will be embraced eventually in one general formula—probably some modification of Galton's Law of Ancestral Inheritance, and that others will be embraced in Mendelian formulæ.

We propose, then, to restrict attention to three frequently occurring modes of hereditary resemblance, which are called *blended*, *exclusive*, and *particulate*.

§ 2. *Certain Necessary Saving Clauses*

Before we define and illustrate the three commonest modes of inheritance, we must, at the risk of reiteration, notice certain saving clauses.

We have seen that cases of apparently very complete hereditary resemblance may be illusions due to our inability to appreciate the differences that really exist; but on the other hand, we must guard against the error of supposing that the frequently conspicuous differences between offspring and their parents necessarily means an incompleteness in the inheritance itself. The fact that the resemblance often reappears in the third generation shows that the incompleteness is often *not in the inheritance*, but simply in its *expression*. The characters were probably there *in posse* in the germinal matter, but they were neutralised, kept latent, silenced—we can only use metaphors—by other characters, or else they never met with the stimulus necessary

for their expression in development. We can imagine the son of a lavish millionaire reacting to plain living, the superficial inference that the money had been lost, and the contradiction of this in the third generation.

Similarly, when a male offspring is compared with the mother, a female offspring with the father, it is important to bear in mind that the difference in sex may account for some of the apparent differences in detailed characters. Through functional correlation, the differentiation of sex may bring about the non-expression or the modified expression of a peculiarity which was none the less transmitted in its entirety as the third generation may demonstrate.

Another fact that must be borne in mind is the difficulty of distinguishing even with probability between hereditary and acquired resemblances. The Alpine plants which Nägeli transplanted to a southern garden were changed by their new surroundings; their descendants were likewise changed, and the new characters reappeared with constancy generation after generation. But this was acquired or modificational, not hereditary or innate resemblance, as was shown by the fact that removal from the garden to poor gravelly soil was followed by a reappearance of the original Alpine characteristics. Some interesting cases have been alleged where the reappearance of the Alpine characters was not immediate, but *gradual*. We require, however, more circumstantial details in regard to these cases.

§ 3. *Blended Inheritance*

In this mode the special characters of the two parents are intimately mingled in the offspring. The colour of the hair may be an almost precise average between that of the blonde mother and that of the black-haired father. In repose the boy's face may seem markedly paternal; it is moved with emotion, and he is his mother's image. This blending is particularly well

seen in some plant hybrids, where the offspring shows in leaf-venation, in size of epidermic cells, in number of stomata, in length of style, in degree of hairiness, and so on, what seems like an accurate mean of the two parents. Prof. J. M. Macfarlane has given some beautifully precise data regarding the blending of characters in plant hybrids.

When in any given character of the offspring we can detect

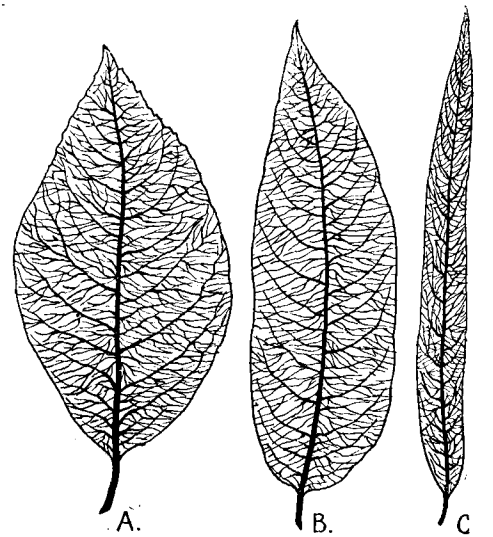

FIG. 24.—Leaves of Willow: A, of one parent; C, of the other parent; B, of the hybrid intermediate between them. (After Wiesner.)

both maternal and paternal peculiarities, we call the inheritance *blended*; but there may be quantitatively more of the maternal quality or of the paternal quality expressed, and then we say that in the blended inheritance or in its expression one of the two parents is *prepotent*. An increase in the predominance of the characteristics of one parent leads to the second common mode of inheritance, which we call *exclusive*.

§ 4. *Exclusive Inheritance* (*Unilateral, Absolutely Prepotent, or Preponderant*)

When in the expression of the biparental inheritance there is, as regards a given character, an absolute prepotency on one side or the other, or, conversely, an apparent reduction of the maternal or paternal peculiarities to zero, the inheritance is called *exclusive*. The terms "unilateral," "absolutely prepotent," or "preponderant" are also used. This mode of inheritance is oftenest seen in regard to particular characters, but it is sometimes consistently illustrated in so many parts of the organism that observers say of the whole offspring that it favours its sire, or that it takes after its mother.

In reference to a few characters a general statement may sometimes be made with security to the effect that, on the average, the father is prepotent in certain respects and the mother in others. Thus, in regard to stature of human beings (in Britain), it seems certain that the father is usually prepotent; that is to say, on the average children attain to a stature which is nearer that of the father than that of the mother. But every statement of this sort must be based on carefully collected statistics, and not on the "impressions"—however strong—which breeders have often formulated as laws.

There are many popular generalisations which ascribe to each of the parents the power of transmitting particular characteristics. Thus, the father is supposed to have to do with external form, the mother with temperament and the organs of vegetative life. While particular statements in respect to this are interesting and should be accumulated in as large numbers as possible, almost all the generalisations, including the one instanced, are mere guesses. At present, we can only say that in some cases the expression of the inheritance as a whole, or in regard to particular characters, may resemble one parent more or less exclusively. In other words, the father sometimes seems absolutely

prepotent, the mother sometimes seems absolutely prepotent, but the characters in regard to which the prepotency is exhibited usually vary from case to case. Goethe may have been quite accurate in saying :

> Vom Vater hab' ich die Statur,
> Des Lebens ernstes Führen;
> Vom Mütterchen die Frohnatur
> Und Lust zu fabuliren.

But this cannot be generalised as a law of inheritance!

There seems to be a widespread belief among breeders that external form depends upon the father, while temperament and visceral organs depend upon the mother. But this does not stand examination. Nor can we rely with security on the opinion of many horse-breeders—*e.g.* Stephens—that the sire almost always counts for most all round; for we have to correct this by remembering that the sire, as an inbred animal of long pedigree, is naturally "prepotent." Buffon pointed out that the mule resembles the father ass more than the mother mare, and the hinny resembles the father horse more than the mother ass; but he dealt only with superficialities. Crossings between humped zebu cattle and those without humps show that the hump is inherited in some degree, whether it was possessed by the ox or the cow; and the same is true in regard to camels with one or two humps, and in regard to crossings of wild boar and sow or *vice versâ*.

There is no doubt that what looks like well-marked "unilateral inheritance" is not infrequent, where the son is, as they say, the very image of his father, or the daughter the reflection of her mother; or, even more frequently, where the inheritance is, as they say, "crossed," the son taking after the mother, and the daughter after the father. But to generalise the latter into a formula, as some dog-breeders have done, "Chien de chienne, et chienne de chien," is quite illegitimate. The result will depend

on which of the parents has the mysterious quality of "prepotency"; and it may be that the father is "prepotent" in regard to some of the characters and the mother in regard to others. A negro in Berlin had by a white woman seven daughters who were markedly mulatto, and four sons who were white; the inheritance was "crossed," but other cases forbid us from making any generalisation.

It must be carefully kept in view that where the expression of the inheritance markedly follows one parent, it does not in the least follow that the corresponding contributions from the other parent have been lost. It may be that the latter will reappear in the next generation, having simply remained latent in the custody of the germ-cells. And again, there are cases on record where the young boy resembled the mother and the young girl the father; but as they grew up, the likeness was reversed—*i.e.* resemblances formerly obscure became dominant. Such cases seem to warrant our insistence on the distinction between the inheritance and the expression of the inheritance.

Apart from a few cases well established statistically, such as the prepotency of the father as regards stature in British families, it is at present illegitimate to make general statements as to exclusive inheritance. Whether the offspring takes after the father or the mother in respect to particular characters probably depends on the more or less unpredictable relative strengths of the corresponding parental contributions to the inheritance.

Instances.—(*a*) De Quatrefages * discusses the well-known case of Lislet-Geoffroy, a corresponding member of the Institute of France. He was the son of a Frenchman and a not very intelligent negress, and inherited physical negroid characters from his mother and high intellectual and moral qualities from his father. Allowance must, of course, be made for education, but it seems fair to say that in this case the father was prepotent as regards the cerebral endowment of the son.

* *Introduction à l'Étude des Races humaines*, p. 184.

(*b*) In regard to his ancestry, Huxley wrote to Havelock Ellis * as follows: "We are mainly Iberian mongrels, with a good dash of Norman and a little Saxon. . . . My father was a Warwickshire man; my mother came of Wiltshire people. Except for being somewhat taller than the average of the type, she was a typical example of the 'Iberian' variety—dark, thin, rapid in all her ways, and with the most piercing black eyes I have ever seen in anybody's head. Mentally and physically (except in the matter of the beautiful eyes) I am a piece of my mother, and, except for my stature, which used to be 5 ft. 10 in., I should do very well for a 'black Celt'—supposed to be the worst variety of that type. My father was fresh-coloured and grey-eyed, though dark-haired; good-humoured, though of a quick temper; a kindly man, rather too easy-going for this wicked world. There is a vein of him in me, but the constituents have never mixed properly." In this case, it may be fairly said that the mother was markedly prepotent.

(*c*) Herbert Spencer did not think that he took after his mother except in some physical features. "Whatever specialities of character and faculty in me are due to inheritance, are inherited from my father. Between my mother's mind and my own I see scarcely any resemblances, emotional or intellectual." He inherited his father's nervous weakness, but his "visceral constitution was maternal rather than paternal." †

§ 5. *Particulate Inheritance*

In many cases it may be seen that the peculiarities of the two parents do not blend, but are separately expressed in different parts of the same organ or system. The combination is, as it were, too coarse-grained to be called a mixture or a blend. This is termed *particulate* inheritance.

A familiar instance is a piebald foal—the progeny of a dark-coloured sire and a light-coloured mare. The paternal hair is seen in some parts, the maternal hair in other parts. "Eye-colour is generally exclusive, but we get one or two cases per

* Havelock Ellis, "Huxley's Ancestry," letter to *Nature*, lxiii. (Dec. 6, 1900), p. 127.

† *Autobiography*, 1904, vol. i.

thousand in man, in which either the two irises differ in colour, or the one iris shows different patches of colour" (Pearson, 1900, p. 452). The case of an English sheep-dog with a paternal eye on the one side of its head and a maternal eye on the other is vivid enough.

In hybrids there are many instances of particulate inheritance. Thus Sanson notes that in the hybrid cattle of Nivernais, the same beast may have a horn of the Durham type on one side and a horn of the Charolais type on the other. We have already alluded to the hybrid Adam's laburnum (*Cytisus adami*), which bore pink flowers (a blend) on some branches, yellow flowers (of one parent, *C. laburnum*) on other branches, and purple flowers (of the other parent, *C. purpureus*) on other branches.

When there is a marked difference in the pedigree, the vigour, the age—in short, in the constitution—of the two parents, the same mode of inheritance may be illustrated in a succession of offspring. Thus an inbred sire, paired with a commonplace mate, may be prepotent birth after birth; or a young mother mated with a worn-out male may have it all her own way in regard to inheritance, as well as in much else. On the other hand, when there are no such marked differences between the parents, the inheritance may be a blend in one offspring, exclusive in another, particulate in a third. Moreover, in the same offspring, different sets of characters may illustrate different modes of inheritance. Thus we see that these modes of inheritance are merely useful descriptive terms, helping us to keep our facts in order, but not directly aiding us in their interpretation. They point to the need of some unifying conception, which shall enable us to understand how all these alternatives are possible.

Postponing this, however, we shall simply notice a few facts which indicate that much depends on the condition of the two gametes when they unite in amphimixis.

In large families there is sometimes observable an interesting change in the direction of preponderance in the successive

children. With a virile middle-aged father and a much younger mother, the older children may be markedly paternal in the expression of their inheritance, the younger children as markedly of the maternal type. The Benjamin is the mother's very image, and after the father's own heart.

Prof. Cossar Ewart records the case of a very young pigeon of hooded or frilled breed which was mated with an old one not decorated with hood or frill. The result was that the first young were smooth-headed and smooth-breasted, but those of later broods had the specialised characteristics of the mother.

Similarly, the first fertilised, almost immature ova of a rabbit, liberated by an ovulation subsequent to the first pairing, resulted in offspring which took after the male. If, on the other hand, a doe is served, not at the right time, but a week or ten days later, the young are all exactly like the mother.

Such facts point to the conclusion that the expression of inheritance follows the parent whose germ-cells are the riper at the time of fertilisation—an inference to which we shall return in discussing germinal selection.

The inference is further supported by Vernon's experiments in the hybridisation of sea-urchins, for he showed that the characters of the offspring incline to be those of the species whose gametes were relatively the more mature when fertilisation occurred.

§ 6. *Summary of Alternatives*

When parents of different species, varieties, or stocks are crossed, the progeny is usually referable to one of the following categories :—

(1) It may be a combination of the paternal and maternal characteristics, either (A) an intimate *blend*, or (B) a blend with preponderance in favour of either parent, or (C) a particulate com-

bination, paternal in some parts, maternal in others. Illustrated, for instance, (A) in crossing two species of willow, (B) in crossing humped cattle and those without humps, and (C) in piebald horses.

(2) It may be exclusively paternal or maternal as far as the expression in development shows. The paternal or maternal contrasted characteristics may be dominant or recessive. That both are present in the inheritance, though not in the expression of the inheritance, may be proved by the next generation—often illustrated when a "prepotent" sire is put to a commonplace female.

(3) In cases of Mendelian inheritance, the offspring are exclusively of one of the parental types as regards one or more unit characters. The corresponding unit characters are held latent or recessive, and the dominant characters alone find expression. But if these "hybrids" are inbred, the next generation shows a reappearance of pure parental types both dominant and recessive—both breeding true—and a number of forms—*like* pure dominants—which, when inbred, again split into pure dominants, pure recessives, and "impure" dominants. Moreover, in typical cases the proportions in the progeny of the "hybrids" always approximate to the formula 1 pure dominant : 2 impure dominants : 1 pure recessive. Illustrated for instance in crossing tall peas and dwarf peas, bandless and banded snails.

(4) It may resemble a grandparent or remoter ancestor more than it resembles the immediate parents. Thus in crossing distinct races of pigeons, a return to the rock-dove type has been often observed (Darwin and many others); similarly, crossing of fowls may recall the original jungle-hen type (Darwin); albino mice and waltzing mice yield grey mice (G. von Guaita); crossing of "Lindenschwärmer" and Peacock-eye butterflies results in progeny like the phylogenetically older "Lindenschwärmer" (Standfuss). In some cases these "reversions" or "atavisms" may be interpreted in terms of the Mendelian Rule.

(5) It may be something apparently new—a "mutation"—a novel position of organic equilibrium, as in De Vries's evening primrose (*Œnothera lamarckiana*). But inquiry must always be made to discover whether the apparent newness is not really a new combination of items in the inheritance.