CHAPTER II

VARIATION

We have seen that the subjects of Heredity and Variation are so closely connected that one cannot be considered apart from the other, for without *variation all the offspring of the same parents would* be exactly alike, and the study of heredity would resolve itself into an investigation of the cause of this likeness. But the actual problem is much less simple; it includes the questions how and why the members of a family may differ from one another, and according to what rules and by what means these differences are transmitted to later generations. In practice therefore the study of heredity is the *study of the manner and cause of the inheritance of* variations, and hence the nature of variation must be examined before enquiry into its transmission.

Before the time of Darwin variations were frequently regarded as abnormalities, inconvenient to the systematist and of relatively small importance. Every species was supposed to conform to the type originally created, and divergences from this type were regarded as imperfections. But it was obvious that there was always more or less fluctuation about the type in different individuals, and breeders of plants and animals made use of this want of uniformity to select the best specimens and so to improve the race. The Natural Selection theory of Darwin and Wallace supposes that a process comparable with this takes place in nature, and so brings about the adaptations of natural species.

Of the causes which induce variation nothing definite was known, but Darwin's belief was generally accepted that it is due to changes in environment acting directly or indirectly on the organism. He regarded the action of such changes as cumulative through a number of generations, so that its effect in producing variation might not be visible until the change had acted on several generations. This belief was founded on the observation that animals bred in captivity appear to be much more variable than in the wild condition, and the changed conditions of life are supposed to induce the variation. But species in nature are not by any means subject to uniform environment, and thus their variability was ascribed to similar causes.

Darwin and Wallace pointed out that variation occurs in all parts of every species, that it appears to occur in every possible direction, and to every extent from very small to considerable range. They therefore founded their theory on this type of variability rather than on the occurrence of considerable 'occasional variations' which are not connected with the type by a series of intermediates. It was not, however, until after the theory of Natural Selection had obtained general recognition, that any detailed study was undertaken of the actual frequency and extent of variation, and its mode of occurrence.

The accurate investigation of variation has thus been in progress only for some twenty or twenty-five years, and according to the methods adopted students have become divided into two somewhat distinct schools. One of these has devoted itself rather to the attempt to observe and classify the different kinds of variation, and the other, generally called the 'biometrician' school, to measure its frequency and range. It will be convenient to consider the results obtained by the second method first.

If a character is chosen which can be accurately measured, such as human stature, and a sufficiently large number of individuals are observed, it will commonly be found that there is considerable range of variation, and that every gradation in size occurs between the smallest and largest. Such variation is spoken of as 'continuous,' as opposed to 'discontinuous' variation in which individuals of two kinds occur, which are not connected by intermediates. Further, in cases of continuous variation it will appear that one size is more common than any other, and, in the simplest cases, that the individuals are progressively rarer as the size of the structure considered diverges more and more from the most frequent value. The most frequent condition is named the 'mode,' and its size the 'modal value' for the character. For example, if the heights of a large number of men were measured, it might be found that they ranged by every gradation from 60 to 76 inches. If the measurements were taken to the nearest inch, it might then be found that a greater number had a stature of 68 inches than any other height, that the next most frequent heights were 67 and 69 inches, and that the more the stature differed from 68 inches in either direction, the fewer would be the men having that measurement. This could be represented graphically by arranging vertical lines representing the heights of every man in order of their height; a line joining their tops would then rise rapidly at the lower end, would be nearly flat as it passed over the men having heights near the 'modal value' of 68 inches, and would rise again steeply to the exceptionally tall men at the upper end of the row (fig. 1). [13][1]

A more instructive method of graphically repre-

[1] For references see the end of the Volume.

senting the distribution of variation is to take a base-line and divide it into equal parts, each representing an equal increment in the structure measured. From each division of the base-line a vertical line is drawn representing by its length the number of individuals having that measurement.

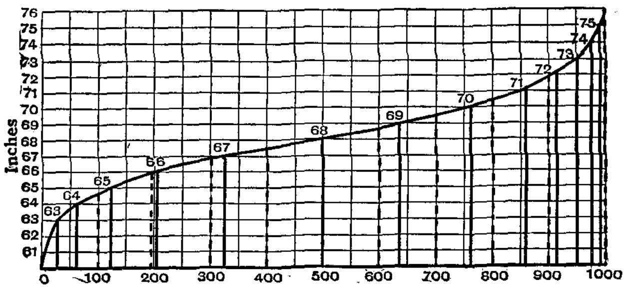

Fig. 1. Curve illustrating stature, the vertical scale representing heights above 60 inches, the horizontal scale numbers of individuals (up to 1000).

In the imaginary case taken above, the base-line would have 17 divisions representing successive heights of from 60 to 76 inches; at each division a vertical line is drawn which by its length represents the percentage of the population which have that height (fig. 2). By joining the tops of the perpendiculars (ordinates) a curve, or more strictly a polygon, is obtained which graphically represents the distribution of the variation among the population measured. The highest point of the curve represents the mode for the character, and the extremes of variation are where it touches the base-line. The more numerous are the subdivisions into which the

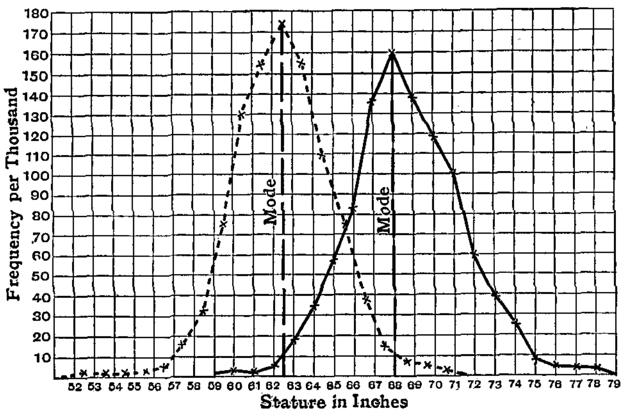

Fig. 2. Curves showing distribution of stature in women (mothers) —dotted line; and in men (fathers)—continuous line. The curves approach the 'normal curve.' (Data from Pearson.)

variable character is classified, the more nearly the line joining the tops of the ordinates will approximate to a smooth curve; e.g. if the population were measured to the nearest quarter of an inch instead of to the nearest inch there would be four times as many ordinates and the curve would be nearly smooth.

It is clear that a curve of this kind can be used for comparing the variability of different characters, for the greater the variability of the population the wider will be the base; consequently the curve for a very variable character will be relatively low and wide, that for a slightly variable one measured in the same scale will be tall and steep. A curve of this kind, which is quite similar on either side of the longest perpendicular ('median,' representing the modal value), may be obtained by plotting any *measurements which vary fortuitously* around a most frequent value, and such a curve is called a 'normal curve.' For example, if a large number of beans including equal numbers of white ones and black ones were placed in a sack, and drawn out ten at a time without selection of colour, most frequently five white and five black would be drawn, less often six of one colour and four of the other, more rarely seven and three and so on to the rarest case of ten of one colour. If the numbers of white beans in a draw are plotted along the base-line, and the ordinates represent the number of draws for each combination, a polygon approaching the normal curve will be obtained. Variation which gives a normal curve when plotted in this way is spoken of as normal variation.

As mentioned above, the steepness of the curve is a measure of variability, and this can be expressed by taking a point in the curve, the perpendicular *from which to the base-line divides the area, enclosed* by the curve, the median and the base-line, into two equal parts. Or, differently expressed, the perpendicular divides the curve in such a way that the number of individuals between it and the mean is the same as that between it and the extreme. The distance of this perpendicular may be used as a measure of the variability of the character considered, *for clearly the greater the variability (and thus the* flatter the curve), the further this perpendicular will be from the median[1].

In many variable characters, the frequency of variation below the mode is not exactly equal to that above it, in which case the curve will be steeper on one side of the mode than on the other, and the average value for the character ('mean') will not be identical with the mode. For example, if the variation in the number of children in a family were plotted in this way, the sizes of families would range from 0 to about 20, but the most frequent number would perhaps be four. Four would then be the

[1] In practice, not this perpendicular, but another rather further from the median is used, which for practical purposes is more convenient. The distance of this perpendicular, measured in units of the horizontal scale, is called the 'standard deviation' and is regularly *employed as a measure of variability.*

modal value, but the average or mean might be about six; the curve would rise steeply to the mode, and fall away more gradually to the maximum number (fig. 3). Such a curve is described as 'skew.' In

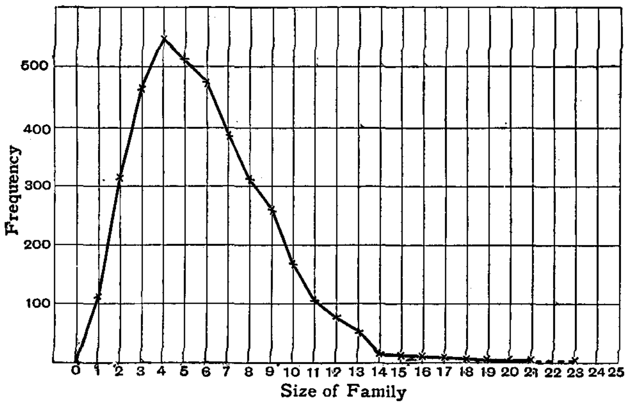

Fig. 3. Curve showing distribution of size of 3837 families in America containing deaf-mutes. (After Schuster, 'Hereditary Deafness.' *Biometrika*, Vol. IV. 1906, p. 474.)

extreme cases the mode is at one end of the curve, when variation takes place only on one side of it, e.g. in the marsh-marigold, the most frequent number of 'petals' is five, but there may rarely be six, seven or eight, but practically never less than five, so that in plotting the frequency a 'half-curve' is obtained (fig. 4).

Another rather frequent condition is that the curve has two maxima or modes (fig. 5), indicating that a large number of individuals have a low measurement, a less number are intermediate, and again a *larger number have a higher measurement.* Species which vary in this way are called 'dimorphic,' or if

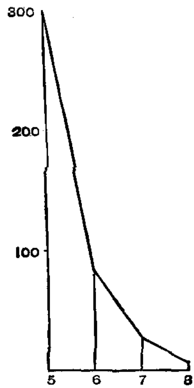

Fig. 4. 'Half-curve' representing the number of 'petals' on 416 flowers of the marsh-marigold (*Caltha palustris*). (After de Vries.)

there are more than two peaks to the curve, 'polymorphic.' Further, it is possible that the two parts of the curve should be entirely separate, if intermediates between the low and high groups are completely wanting. This type of variation is spoken of as 'discontinuous' in contrast to the 'continuous' variation hitherto considered. It is possible that dimorphic cases in which intermediates exist are really essentially discontinuous, but that the two groups into which the species is divided each exhibit continuous variation about the mode for the group, to such an extent that the higher members of one

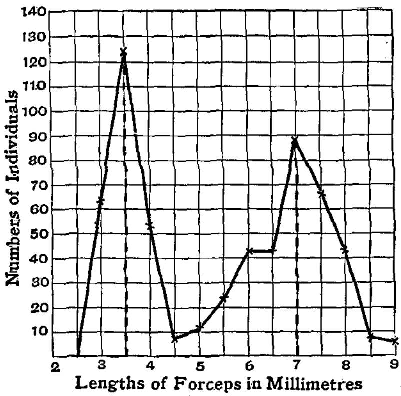

Fig. 5. Curve with two modes, representing frequency of lengths of forceps of male Earwigs from the Farne Islands. (After Bateson.)

group overlap the lower of the other. For example, if the modal (most frequent) stature for a race of men were 68 inches, and for the women 62 inches, it might happen that on plotting a frequency curve for the stature of adults including both sexes, a curve would be obtained having two maxima, one near 62 and another near 68. Yet the stature might be a definite sexual character, and hence essentially as discontinuous as the sexes themselves. This distinction between continuous and discontinuous variation may seem unimportant in itself, but when its inheritance is considered the distinction becomes of the first importance.

Clearer examples of discontinuous variation are given by such characters as colour, or by organs which are repeated in series, such as vertebrae and ribs, the segments of a worm or the petals of a flower. When variation occurs in this latter group it is generally complete, so that the different forms are visibly discontinuous. In the case of colour in the skin or hair in animals, or petals of flowers, discontinuity is sometimes less apparent, and grading frequently occurs, but even in apparently graded cases the inheritance of the character may often reveal discontinuity. For example, a piebald animal might be thought to be intermediate between the fully-coloured and albino (white with no pigment), but breeding tests would at once show that piebaldness was an independent character, which cannot be regarded as in any sense intermediate between the other two conditions except in general appearance. The same applies to such cases as the 'silver' cat or rabbit, or the pale purple sweet-pea; the cause of the pale colour is entirely distinct from the cause of the absence of pigment in the white varieties of those species.

The recognition of the importance of discontinuity in variation, which we owe chiefly to the work of Bateson in England and De Vries in Holland, is one of the chief advances which the study of the subject has made since the time of Darwin.

One other distinction between different kinds of variation must be mentioned here, which will be discussed more fully in subsequent chapters. The kinds of variation mentioned above are all *inborn*, or inherent in the individual and to a great extent independent of its manner of life. But it is well known that the continued use of an organ or structure, or the prolonged action upon it of some external stimulus, may alter its form or cause it to assume a condition different from that which it would have had if these influences had not acted. In general, an organ tends to adapt itself either to the uses to which it is put or to the action of the environment which surrounds it. The muscles of a limb used for strenuous work increase in size and strength, or a part of the skin continually exposed to bright light develops a deeper colour than if it is covered. The converse process is also true; an organ which is not used or exposed to its normal stimuli tends to diminish, and become less adapted to the use to which it is normally put. Such characters as these, arising in response to a stimulus, and not appearing in its absence, are technically called 'acquired characters,' a phrase which it will be necessary to use rather frequently in the following pages. As a rule, such 'acquired characters' are adaptive, that is, they render the organism or structure better fitted to its surroundings than if they had not been developed. The older students of heredity never doubted that these acquired characters were inherited as strongly as the inborn characters discussed above, but since the publication of Weismann's theory of heredity (see Appendix I) with the great body of evidence which he has collected on the other side, opinion has turned increasingly towards the belief that acquired variations are not transmitted. Weismann regards the germ-cells as essentially distinct from the rest of the body, so that acquired modifications of the body cannot be transmitted because the germ-cells are not affected. The germ-cells collectively, or rather that part of them which is concerned with the transmission of hereditary characters, he calls 'germ-plasm,' the rest of the body consisting of 'body-plasm' (or 'soma'), and he regards 'acquired' modifications as affecting body-plasm only. A developing germ-cell gives origin to both germ-plasm and body-plasm of a new individual, and hence characters borne by the germ-plasm appear in the body; but since body-plasm cannot be converted into germ-plasm, modifications of the body cannot be transmitted to offspring.

The possible inheritance of acquired characters is treated more fully in a later chapter.