CHAPTER I.

ARRANGEMENT OF EVIDENCE.

THE cases of Meristic Variation, here given, illustrate only a small part of the subject. The principles upon which these have been chosen may be briefly explained. It was originally intended to give samples of the evidence relating to as many different parts of the subject as possible, so that the ground to be eventually covered might be mapped out, leaving the separate sections of evidence to be amplified as observations accumulate. This plan would be the most logical and perhaps in the end the most useful, but for several reasons it has been abandoned. I have chosen a different course, first, because during the progress of the work opportunities occurred for developing special parts of the evidence; secondly, since isolated observations have no interest for most persons, it is more likely that the importance of the subject will be appreciated in a fuller treatment of special sections, than in a general view of the whole; and lastly, because as yet the attempt to make an orderly or logical classification of the phenomena of Merism, however attractive, must be so imperfect as to be almost worthless. For these reasons I have decided to treat more fully a few sections of the facts, hoping that in the course of time similar treatment may be applied to other sections also. The sections have been chosen either because there is a fairly large body of evidence relating to them, or on account of the importance or novelty of the principles illustrated.

As far as possible I have described each case separately, in terms applicable specially to it, deductions or criticism being kept apart. The descriptions are written as if for an imaginary catalogue of a Museum in which the objects might be displayed¹. This system, though it entails repetition, has, I believe, advantages which cannot be attained when the descriptions are given in a comprehensive and continuous form. In speaking of subjects, such as supernumerary mammæ, or cervical fistulæ, where the evidence has been exhaustively treated by others, and upon which I can add nothing, it has not seemed necessary to follow this system, and in such cases connected abstracts are given.

¹ Cases of special importance are marked by an asterisk.

As the evidence here presented consists, as yet, only of specimen chapters in the Natural History of Meristic Variation, and does not offer any comprehensive view of the whole subject, no strict classification of the facts is attempted. The evidence of Meristic Variation relates essentially to the manner in which changes occur in the number of members in Meristic series. Such numerical changes may come about in two ways, which are in some respects distinct from each other. For instance, the number of legs and body-segments in *Peripatus edwardsii* varies from 29 to 34¹: here the variation in number must be a manifestation of an original difference in the manner of division or segmentation in the progress of development. The change is strictly Meristic or divisional. On the other hand, change in number may arise by the Substantive Variation of members of a Meristic series already constituted. For example, the evidence will shew that the number of oviducal openings in Astacus may be increased from one pair to two or even three pairs. Here the numerical variation has come about through the assumption by the penultimate and last thoracic appendages, of a character typically proper to the appendages of the antepenultimate segment of the thorax alone. Now there is here no change in the number of segments composing the Meristic series, but by Substantive Variation the number of openings has been increased.

The case of the modification of the antenna of an insect into a foot, of the eve of a Crustacean into an antenna, of a petal into a stamen, and the like, are examples of the same kind.

It is desirable and indeed necessary that such Variations, which consist in the assumption by one member of a Meristic series, of the form or characters proper to other members of the series, should be recognized as constituting a distinct group of phenomena. In the case of plants such Variation is very common and is one of the most familiar forms of abnormality. MASTERS, in his treatise on Vegetable Teratology², recognizes this phenomenon and gives to it the name "Metamorphy," adopting the word from Goethe. As Masters says, so long as it is only proposed to use the word in Teratology, no great confusion need arise from the fact that the same term and its derivatives are used in a different sense in several branches of Natural History. But if, as I hope, the time has come when the facts of what has been called "Teratology" will be admitted to their proper place in the Study of Variation, this confusion is inevitable. In this study, besides, this particular kind of variation will be found to be especially important and I believe that in the future its significance and the mode of its occurrence will become an object of high interest. For this reason it is desirable that the term which denotes it should not lead to misunderstanding, and I think a new term is demanded.

SEDGWICK, A., Quart. Jour. Micr. Sci., 1888, XXVIII. p. 467.
MASTERS, M. T., Vegetable Teratology, p. 239.

For the word 'Metamorphy' I therefore propose to substitute the term **Homœosis**, which is also more correct; for the essential phenomenon is not that there has merely been a change, but that something has been changed into the likeness of something else.

In the cases given above, the distinction between Homeotic Variation and strictly Meristic Variation is sufficiently obvious, but many numerical changes occur which cannot be referred with certainty to the one class rather than to the other. Such cases are for the most part seen in Vertebrates: for in them what may be called the *fundamental* numbers of the segments are not constituted with the definiteness found in Arthropods or in the Annelids, and several Meristic series of organs are disposed in numbers and positions independent of, or at least having no obvious relation to those of the other Meristic series. The number and positions of mammæ, or stripes, for instance, need not bear any visible relation to the segmentation of the vertebræ &c. The repetition of members of such a series may thus not coincide with, or occur in multiples of the segmentation of other parts in the same region. When such is the case, when the segmentation of one series of organs bears no simple or constant geometrical relation to the segmentation of other systems, it is not always possible to declare whether a numerical change in one of the systems of organs belongs properly to the first or the second of the classes described above. It is likely enough that in such a case as that of mamma, there may sometimes be an actual Meristic division and subsequent separation of the tissues already destined to form the mammæ, occurring in such a way that each comes to take up its final position, and indeed the numerous cases in which such division has been imperfectly effected go far to prove that this is the case. But, on the other hand, it is not possible to know that the division did not occur before any tissue was specially differentiated off to form mamma, and that the separation may be as old even as the division of the mammæ of the right side from those of the left, a process which almost beyond question occurs in the segmentation of the ovum. The distinction between these two alternatives is thus one rather of degree than of kind, and it is only in such forms as the Arthropods, the floral organs of some Phanerogams and the like, where the members of the several Meristic series have definite numbers, or coincide with each other, that this distinction is easily recognized. For this reason I do not think it well to attempt to carry out any classification of the evidence based on this distinction.

In the foregoing remarks I am aware that a very large question, which lies at the root of all accurate study of Meristic Variation, has been passed over somewhat superficially, but I scarcely think a fuller treatment possible in the present state of knowledge of the physics of Division, and in the absence of thorough observation of the developmental history of those tissues which ultimately become differentiated to form members of such non-coincident or independent Meristic series.

Some years ago', in the course of an argument that Balanoglossus should be considered as representing some of the ancestral characters of Chordata, I had occasion to refer to some of these difficulties, and especially to the different characters of the two kinds of segmentation; that of the Annelids, in which the repetitions of the organs belonging to the several systems are coincident, and, on the other hand, that of the Chordata, for example, in which this coincidence may be irregular or partial. At that time I was of opinion that these two sorts of segmentation may, in certain cases, have had a different phylogenetic history, and have resulted from processes essentially distinct. It appeared to me that we should recognize that, in the Annelids on the one hand, segmentation of the various systems of organs had been coincident from the beginning, while in the Chordata the segmentation had been progressive and had arisen by segmentation or repetition of the organs of the several systems independently. The reasons for this view were derived chiefly from the fact that it is possible to arrange the lower Chordata in order of progressive segmentation of the several systems. In particular such treatment was shewn to be applicable to the central nervous system, the vertebral column and the mesoblastic somites, and in these cases it was maintained that the evidence of the lower forms of Chordata goes to shew that segmentation had occurred in these systems one after another, and that their segmentation was not derived from a form having a complete repetition of each part in each segment : that these forms, in fact, shewed us the history of this progress from a less segmented form to one more fully segmented.

The views then set forth have met with little acceptance. Those who are occupied with the search for the pedigree of Vertebrates still direct their inquiries on the hypothesis, expressed or implied, that in the ancestral form there was a series of complete segments, each containing a representative of each system of those organs which in the present descendants appear in series. It is thus supposed that each segment of the primitive form must have been a kind of least common denominator of the segments of its posterity. The possibility that the segmentation of Vertebrates may have arisen progressively is, indeed, scarcely considered at all.

Though in the light of the study of Variation, it now seems to me that the discussion of these questions must be indefinitely postponed, and that there are radical objections to any attempt to interpret the facts of anatomy and development in our present ignorance of Variation, I have seen no reason to depart from the view expressed in the paper referred to: that interpreted by the current methods of morphological criticism, the facts go to shew that the segmentation of the Chordata differs essentially from that of the Annelids &c., and that it has arisen by progressive segmentation of the several systems of an originally unsegmented form. To those who hold as Dohrn, Gaskell, Marshall and others have done, that the evolution of Vertebrates has

¹ Quart. Jour. Micr. Sci., 1886.

been a progress from a more fully segmented form to forms less segmented, I would again point out that this view is in direct opposition to the indications afforded by the lower Chordata, which are *less and* not more segmented than the higher forms.

The hypothesis of an ancestor made up of complete segments is resorted to because it is felt to be difficult to conceive the progressive building up of a segmented form, but on appeal to the facts of Variation the evidence will clearly shew that Repetition of parts previously existing is a quite common phenomenon; that such repetition may occur in almost any system of organs; and lastly that such new repetitions may be coincident in the several systems. To argue moreover that these repetitions, for instance that of oviducal apertures in *Astacus*, of mammæ or cervical ribs in mammals are "reversions," leads to absurdity, for on the same reasoning, the occurrence, in the Crab, of a third maxillipede formed as a chela, would shew that these appendages had been originally chelæ, that the occurrence of petaloid sepals shews that the sepals had originally been petals, and so forth.

These considerations will suffice to illustrate the great difference of degree, if not of kind, which probably exists between these two kinds of segmentation, that which arises by the repetition of budlike segments, each containing parts of many systems on the one hand, and the progressive and separate segmentation of the several systems on the other. For reasons already given, however, I shall not attempt in this first collection of evidence to separate the facts on these lines. Though some cases can at once be seen to be strictly Meristic while others are plainly Homeotic, many cannot be affirmed to belong to the one group rather than to the other. There is, besides, a serious doubt whether perhaps after all, Homeotic Variation even in its most marked forms, may not ultimately rest on and be an expression of a change in the processes of Division, and be thus, at bottom, strictly Meristic also. In our present ignorance of the physics of Division, this doubt cannot be satisfied, and therefore it will be best to make no definite separation between the two classes of variations, though whenever the nature of a given variation is such that it may at once be recognised as Homeotic, it will be well to specify this.

In the absence of a more natural classification, the material has been roughly arranged with reference to the geometrical disposition and relations of the structures concerned. In the Introduction, Section IV. p. 21, reference was made to the fact that the Symmetry of an organism may be such as to include all the parts into one system of Symmetry, and for such a system the term **Major Symmetry** was proposed. Systems of this kind are seen in the Vertebrates and Echinoderms, for example. On the other hand systems of Symmetry occur in limbs and other separate parts of organisms, in such a way that each such system is either altogether or partially geometrically complete and symmetrical in itself. For example, the toe of a Horse, the arm of a Starfish, the eye-spots of some Satyrid butterflies, &c., are each in themselves nearly symmetrical. To these separate systems of Symmetry the term **Minor Symmetry** will be applied. Minor Symmetries may or may not be compounded into a Major Symmetry. Between these there is of course no hard and fast line.

In each class of Symmetry, Meristic Repetition may occur, and the repeated parts then stand in either

I. Linear or Successive Series.

II. Bilateral or Paired Series.

III. Radial Series.

Parts meristically repeated may thus stand in one or more geometrical relations to each other, and the first part of the evidence of Meristic Variation will be arranged in groups according as it is in one or other of these relations that the parts are affected. In each group cases affecting Major Symmetry will be given first, and those affecting Minor Symmetries will be taken after.

As it is proposed to arrange the facts of Meristic Variation in groups corresponding with these three forms of Meristic Repetition, it will be useful to consider briefly the nature of the relation in which the members of such series stand to each other, and the characters distinguishing the several kinds of series. Reduced to the simplest terms, the distinction may be thus expressed.

In the Linear or Successive series the adjacent parts of any two consecutive members of the series are not homologous, but the severally homologous parts of each member or segment form a successive series, alternating with each other. For example, the anterior and posterior surfaces of such a series of segments may be represented by the series

$A\ldots, AP, AP, AP, AP, \ldots, P.$

The relation of any pair of organs in Bilateral Symmetry differs from this, for in that case each member of the pair presents to its fellow of the opposite side parts homologous with those which its fellow presents to it, each being, in structure and position, an optical image of the other. The external and internal surfaces of such a pair may therefore be represented thus:

E.....I, I....E.

If the manner of origin of these two kinds of Repetition be considered, it will be seen that though both result from a process of Division, yet the manner of Division in the two cases is very different. For in the case of division to form a paired structure, the process occurs in such a way as to form a pair of images, of which similar and homologous parts lie on each side of the plane of division; while, in the formation of a chain of successive segments, each plane of division passes between parts which are dissimilar, and whose homology is alternate. The distinction between these two kinds of Division is of course an expression of the fact that the attractions and repulsions from which Division results are differently disposed in the two cases. It is further to be observed that the distinction, though striking, is nevertheless one of degree, for the two kinds of Division pass gradually into each other. By one or other of these two modes, or by a combination of both, all Meristic Series of Repetitions are formed.

In Radial series, the *Major Symmetry* is built up by radial divisions of the first kind, producing segments whose adjacent parts are homologous, and related to each other as images. Each of these segments is therefore bilaterally symmetrical about a radial plane. There is no succession between the segments, and in a perfectly symmetrical series, Successive or Linear repetitions can only occur in Minor Systems of Symmetry.

The considerations here set forth, though well known, have an importance in the interpretation of the evidence, for the connexion between the geometrical relations of organs and their Meristic Variations is intimate.

An arrangement of the facts with reference to these geometrical relations cannot, of course, be absolute, for it is clear that a Bilateral Symmetry, containing Linear Repetitions may be derived from a Radial Symmetry, and that these figures cannot be precisely delimited from each other; nevertheless this plan of arrangement has still several advantages. Chief among these is this: that it brings out and emphasizes the fact that the possible, or at least the probable Meristic Variations of such parts depend closely on the geometrical relation in which they stand. This is, perhaps, in a word, the first great deduction from the facts of Meristic Variation. The capacity for, and manner of Meristic Variation appear to depend not on the physiological nature of the part, on the system to which it belongs, on the habits of the organism, on the needs or exigencies of its life, but on this fact of the geometrical position of the parts concerned. Linear series are liable to certain sorts of Variation, Bilateral Series are liable to other sorts of Variation, and Radial Series to others again. As I have ventured to hint before, the importance of all this lies in the glimpse which is thus afforded us of the essential nature of Meristic Division and Repetition. Such interdependence between the geometrical relations, or pattern, in which a part stands, and the kinds of Variation of which it is capable, is, I think, a strong indication that in Meristic Division we are dealing with a phenomenon which in its essential nature is mechanical. Since this is a thing of the highest importance, it will be useful to employ a system which shall give it full expression.

Evidence as to Meristic Variation in cell-division and in the segmentation of ova will be spoken of in connexion with the Variation of Radial and Bilateral series.

The second section of evidence is less immediately relevant to the problem of Species; nevertheless it bears so closely on the nature of Merism and on the mechanics of Physiological Division, that in any study of this subject reference to it cannot be omitted. The evidence in question relates first to abnormal repetition of limbs or other peripheral structures, (which in the normal form are grouped into and form part of a system of Symmetry,) such abnormal repetitions occurring in such a way as to lie outside this normal system of Symmetry and unbalanced by any parts within it. This phenomenon occurs in many forms, especially in bilateral animals, and may be exceptionally well studied in the case of supernumerary limbs in Insects and in supernumerary chelæ in Crabs and Lobsters. It will be shewn that such extra parts generally, if not always, make up a **Secondary system of Symmetry** in themselves; and the way in which such a Secondary system is related to the normal or **Primary system** of **Symmetry** of the body from which they spring, constitutes an instructive chapter in the study of Meristic Variation.

More extensive repetitions of this class, when affecting the axial parts of the body, give rise to the well-known Double and Triple Monsters, which, as has often been said, reproduce in the higher animals phenomena which, under the name of fission, are commonly seen in the lower forms. The general evidence as to these abnormalities is so accessible and familiar that it need not be detailed here, and it will therefore be enough to give an outline of its chief features and to point out the bearing of this class of evidence on the subject of Meristic Variation in general.