CHAPTER XXIII.

Secondary Symmetry in Vertebrates.

Remarks on the Significance of Repetitions in Secondary Symmetry: Units of Repetition.

The evidence as to repetition of appendages in vertebrates is of great extent and has been studied by many, but in the morphology of these repetitions there is still much that is obscure. Speaking generally, the phenomena are similar to those seen in Arthropods, but there is no approach to the same regularity. Nevertheless when two extra limbs are present, it is usually possible to recognize that they are together a complementary pair; and if the extra part is apparently a single limb it is, I believe, never a normal limb and may very often be shewn to contain parts of a pair of limbs. The fact that the geometrical relations of the parts are less regular than they are in Arthropods may probably be ascribed in some measure to the circumstance that the surfaces of the vertebrate limbs do not maintain their original relations but are more or less rotated in the course of their development.

In Insects it appeared that repetition of the peripheral parts in Secondary Symmetry was not much more common than repetitions of whole limbs, but apparently this is not the case in vertebrates. Perhaps it would be more true to say that in vertebrates it is only in those extensive repetitions which include the greater part of the limbs beginning from the girdles, that the parts are clearly in Secondary Symmetry. From this circumstance doubt suggests itself whether some of the phenomena of polydactylism, at present regarded as repetitions of digits in Series, may not really be of the nature of Repetitions in Secondary Symmetry (see p. 378). But however this may be, there are, with the exception of some Artiodactyle cases, no examples of paired repetitions of digits or phalanges at all suggesting a comparison with the double extra tarsi &c. of Insects, or the double extra dactylopodites of Crustacea.

In the most usual forms of extra limbs in vertebrates a more or less amorphous pair of limbs, compounded together for a great part of their length, are attached to a supernumerary piece fitted into some part of the shoulder-girdle, or more often into the pelvic girdle.

It is important to notice that though, as many (especially ERCOLANI) have shewn, a complete series can be constructed, ranging for instance from the ordinary pygomelian up to complete posterior duplicity, yet repetition of limbs may be and often is wholly independent of any axial duplicity, being truly a repetition of appendicular parts only.

The question naturally arises whether there is ever an extra limb placed as a single copy of a normal limb of the same side as that on which it is attached. As to this the evidence is not wholly clear, but I incline to think that no case known to me can properly be so expressed. Perhaps the condition which comes nearest to this is exemplified by a case of a Frog fully described by KINGSLEY[1], where a single extra left hind leg is said to have been attached to the left side of the pelvis. It is difficult to question that this was actually the fact, for the figure clearly represents the extra limb as a left leg; but though the muscles are fully described, the bones are not, and it still seems possible that there was in reality some duplicity in the limb. The leg was admittedly abnormal in its anatomy and the naming of the muscles must in part have been approximate.

But though perhaps it should not be positively stated that no *single* extra limb is ever formed in a vertebrate in Succession to the normal limb of the same side of the body, it is certainly true that in the enormous majority of polymelians the extra repetition consists of parts of a complementary pair. These phenomena are thus of interest as bearing upon the morphology of repetitions in Secondary Symmetry, but in all probability are not of the nature of variations in the constitution of the Primary Symmetry.

A just view of the details of these phenomena can only be gained from the specimens or from numerous drawings. The cases of extra limbs in Batrachia may be conveniently studied as exhibiting most of the different kinds of Secondary Symmetries both in the fore and hind limbs. In all, some fifty cases are recorded. These may be found from the following references. The evidence up to 1865 was put together by DUMÉRIL, and an abstract of it is given also by LUNEL, and by KINGSLEY. A fuller bibliography is given by ERCOLANI. The best papers on the subject are marked with an asterisk. I have added a few references of less importance not included in the other bibliographies.

* DUMÉRIL, *Nouv. Arch. Mus. Paris*, 1865, I. p. 309, Pl. XX.

* LUNEL, *Mém. soc. phys. d'hist. nat. de Genève*, 1868, XIX. p. 305, Pl.

[1] *Proc. Bost. N.H.S.*, 1881—2, XXI. p. 169, Pl. II.

* KINGSLEY, *Proc. Boston N.H.S.*, 1881—2, XXI. p. 169, Pl. II.

* CAVANNA, G., *Pubbl. del R. Ist. di Studi super. in Firenze*, 1879, p. 8, *Tav.* I. Four important cases; one, *fig.* 2, apparently resembling Kingsley's in some respects.

* MAZZA, *Atti Soc. ital. sci. nat.*, 1888, XXXI. p. 145, Pl. I.

TUCKERMAN, *Jour. Anat. Phys.*, 1886, p. 517, Pl. XVI.

Cat. Terat. Ser. Coll. Surg. Mus., 1872, No. 23.

HÉRON-ROYER, *Bull. soc. Zool. France*, 1884, IX. p. 165.

BERGENDAL, *Bihang k. svensk. vet. Ak.*, 1889, XIV. Afd. IV. Pl. I.

* ERCOLANI, *Mem. Acc. Bologna*, 1881, IV. p. 810, Pl. IV. Four important cases and very good bibliography.

SUTTON, *Trans. Path. Soc.*, 1889, XL. p. 161, *fig.*

[Three cases in Newts: *Triton cristatus*, JÄCKEL, *Zool. Gart.*, 1881, XXII. p. 156. *Triton tæniatus*, LANDOIS, H., *ibid.*, 1884, XXV. p. 94; CAMERANO, *Atti Soc. ital. sci. nat.*, 1882, XXV].

From these Batrachian cases most of the chief features of the phenomena may be learnt. To those wishing to get a general view of the subject of repetition of Vertebrate limbs in a comparatively small compass the valuable memoir of ERCOLANI quoted above is especially recommended.

Before proceeding to a consideration of the significance of the phenomenon of Repetition in Secondary Symmetry it must be expressly stated that there are in vertebrates a certain number of cases, perhaps even classes of cases, which it is likely differ widely from the rest; but as was said above, the chief difference between the Vertebrate and Arthropod cases lies in the comparative simplicity of the latter. It may be stated further that this greater simplicity of the Arthropod cases consists especially in the maintenance of the relation between the extra pair and some normal limb.

Remembering always the existence of unconformable cases we may, I think, safely gather up from the simple cases several points relating to the problems of Natural History at large. I only propose here to make allusion to those considerations which are not developed in the ordinary teratological treatises.

Of the fact that any regularity can be discerned in these strange departures from normal structure, and of the bearings of this fact on current conceptions of the causes determining the forms of animals it is now hardly necessary to speak further. Other points not before noticed remain.

In the Arthropod cases that were spoken of as 'regular' it was seen that the polarity of the Secondary Symmetries has a definite relation to that of the body which bears them. This is quite in harmony with the supposition that they are related to the normal body somewhat as buds are related to a colony, for in most colonial forms the morphological axes and planes of the buds are definitely related to those of the stock.

But in the Vertebrate cases though there is generally a relation of images between the extra pair, a definite geometrical relation between them and a normal limb is seen more rarely.

That this is so may, I think, be in part at least attributed to the normal twisting of the vertebrate limb, especially of the hind limb, from its original position (see Note on p. 459).

A question brought into prominence by facts of this kind is that of the nature of the control which determines *how much* of a body shall be repeated, or be capable of repetition, in a Secondary Symmetry.

What is a *unit* of repetition?

With repetition of a whole body we are familiar. Apart from the processes of sexual reproduction, we know this total repetition in the many forms of asexual reproduction, whether occurring by budding, or by division either of adult bodies or of embryos[1], and we thus commonly look on the whole body of any organism as in a sense a unit, capable of repetition or of differentiation—the latter especially in gregarious and colonial forms. Again, we familiarly use the conception of cells as units of repetition or of differentiation. Besides these we have come to recognize that members of series of segments are, in their degree, similar units. And generally, the same attribute of separateness may in undefined senses be properly attached to all organs that are repeated in Series, and to appendicular parts especially.

The attribution of some of the undefined properties of "unity[2]" to some at least of these various groups is very ancient, and there can be no doubt that it is in the main a right and useful induction.

The chief interest of repetitions in Secondary Symmetry lies in the fact that they give a glimpse of new light upon the nature of this unity, shewing a new form in which it may appear.

For in Secondary Symmetry there is not a simple repetition of a part in Series, taking its place as a member of that series, but an addition of paired parts, whose intrinsic relation to each other is the same as that of any pair of parts occurring in the Primary Symmetry.

The addition is thus a *unit,* is in form complete in itself, and seems to have no place in the Primary Symmetry of the whole body any more than a late side-chapel—also a unit with its own focus and polarity—had a place in the design of the original architect of the Cathedral.

From analogy, and from general knowledge of vital processes it would I think have been impossible to foresee the very curious indefiniteness of the *quantity* of the parts repeated in systems of Secondary Symmetry. It seems, especially in Arthropod cases,

[1] As a normal occurrence notably in the case of Cyclostomatous Polyzoa of the genus *Crisia* described by HARMER, S. F., *Q. J. M. S.*, 1891, p. 127, *Plates*.

[2] This somewhat incorrect term is used here to express some of the meanings commonly still more incorrectly rendered by the word "*individuality*"—a word etymologically most unhappy in this application to things endowed with divisibility as a conspicuous attribute.

that the repetition may begin from any point in an appendage and include all the parts peripheral to the point of origin. Seeing that the repeated parts are, in their degree, comparable with a whole organism, this indefiniteness is remarkable. We have thus to recognize that the property of morphological "unity" may attach not only to a pair of appendages beginning from the body, or from some definite surface of articular segmentation, but also to a pair of parts having no semblance of morphological distinctness.

Strangest of all is the repetition of the index of Crabs and Lobsters in Secondary Symmetry. The dactylopodite is of course a separate joint. Double extra dactylopodites in Secondary Symmetry present no feature different from double extra tarsi, &c. But the index we think of as merely a large spine or tubercle. It is in no sense a joint or segment. Yet a pair of indices may be added to a normal body. The interest of this fact is in its value as a comment on the principle given on p. 476 that extra parts in Secondary Symmetry contain the structures *peripheral* to their point of origin. The case of extra indices shews that the term peripheral, if it is to include the case of indices, must be interpreted as meaning not morphologically but *geometrically peripheral*[1].

We have spoken of parts in Secondary Symmetry as having no place in the Primary Symmetry of the body. This is on the whole a true statement, but there are a few cases which make it uncertain whether it is absolutely true. These cases are those few where repetitions in Secondary Symmetry were present on appendages of both sides of the body.

Cases of this class were *Odontolabis stevensii*, No. 799, and *Melolontha hippocastani*, No. 795, where such extra parts were present on both antennæ, suggesting that the similarity of the repetition of the two sides is due to the relation of Symmetry between the right side and the left. But against this view may be mentioned the cases *Prionus coriarius*, No. 750, and *Carabus irregularis*, No. 760, where two legs of the *same* side each bore extra parts, and the Lobster, No. 821, having *two* pairs of extra points on one dactylopodite. These cases suggest that bilateral simultaneity in such repetition may perhaps represent merely a general capacity for this form of repetition. The case of *Prionus californicus*, No. 843, would no doubt bear on this question, but unfortunately the facts in that case are scarcely well enough known to justify comment.

[1] A case is given by FAXON (*Harv. Bull.*, VIII. Pl. II. fig. 8) of **Callinectes hastatus** in which the left lateral horn of the carapace, instead of being simple as in normal specimens, had *three* spines. It is just possible that two of these may have been in Secondary Symmetry. All other cases known to me are in appendicular parts.

One further point remains to be spoken of. We have said that a system of parts in Secondary Symmetry is in a sense analogous with a bud, but in one respect the condition of these parts differs remarkably from all phenomena of budding or reproduction that are seen elsewhere. In a bud the various organs always present the same surfaces to each other, or in other words, the planes of division always pass between *similar* surfaces. In Secondary Symmetries this is not the case. As illustrated by the diagram on p. 481, the extra parts may present to each other, or remain compounded by *any* of their surfaces, whether anterior, posterior, or otherwise. This seems to be altogether unlike anything ever met with in animals and plants. It is as if in a bud on a plant two leaves on opposite sides of the axis could in their origin indifferently present any of their surfaces to each other.

It will be remembered that the symmetry cannot be the result of subsequent shiftings, but must represent the original manner of cleavage of the two extra limbs from each other. We must therefore conceive that in the developing rudiment of the two extra limbs either surface may indifferently be external, the polarity being ultimately determined by the relation of the bud or rudiment to the limb which bears it.