CHAPTER XVI.

RADIAL SERIES.

LITTLE need be said in preface to the facts of Meristic Variation in Radial Series. In them phenomena analogous to those of the Variation in Linear Series are seen in their simplest form. Just as in Linear Series the number of members may be changed by a reconstitution of the whole series so that it is impossible to point to any one member as the one lost or added, so may it be in the Meristic Variation of Radial Series: and again as in Linear Series, single members of the series may divide. Between these there is no clear line of distinction.

Next, as in Linear Series, Variation, whether Meristic or Substantive, may take place either in single segments (quadrants, sixths, &c.), or simultaneously in all the segments of the body. For instance, a single eye may be divided into two, or there may be duplicity simultaneously occurring in all the eyes of the disc (see No. 634) and so on.

These phenomena are here illustrated by facts as to the Meristic Variation of Hydromedusæ and of *Aurelia*. The latter is exceptionally variable and in its changes exhibits important features.

Together with these facts as to Variation in Major Symmetries is given an instance of similar Variation in the pedicellariæ of an Echinid, and it will be seen that in this case of a Minor Symmetry the change is perfect and altogether comparable with those found in Major Symmetries of similar geometrical configuration.

The best field for the study of the variations of Radial Series is of course to be found in plants; and in the Meristic Variations of radially symmetrical flowers precisely similar phenomena may be easily seen.

I. Cœlenterata.

*630. **Sarsia mirabilis**¹: normally *four* radial canals, &c. (Fig. 127, I and III). Out of many hundreds of N. American specimens *two* were found with *six* radial canals, six ocelli, and six tentacles,



FIG. 127. Sarsia mirabilis. I and III, the normal form, with four radii, from below and from above. II and IV, an abnormal form with six radii, from below and from above respectively. (From AGASSIZ.)

symmetrically arranged (Fig. 127, II and IV). These specimens were of larger absolute size than the normals. AGASSIZ, L., Mem. Amer. Ac. Sci., IV. p. 248, Pl. v. fig. 5.

¹ Sarsia is the medusa of the Gymnoblastic Hydroid Syncoryne.

- *631. Sarsia sp. Among many thousands examined on the east coast of Scotland one was found having six radial canals, six ocelli and six tentacles. ROMANES, G. J., Jour. Linn. Soc., Zool., XII. p. 527.
- *632. Sarsia sp. A single specimen having *five* complete segments: the only abnormality met with among thousands of naked-eyed medusæ observed, *ibid.*, XIII. p. 190.

There is perhaps in the whole range of natural history no more striking case of the Discontinuity and perfection of Meristic Variation.

Is it besides a mere coincidence, that the specimens presenting this variation, so rare in the free-swimming Hydromedusæ, should have been members of the same genus?

633. Clavatella (Eleutheria) prolifera. This form has a medusa which creeps about on short suctorial processes borne by the tentacles. The number of these tentacles varies from 5 to 8. In the specimens examined by KROHN¹ the number was 6. Most of CLAPARÈDE's² specimens had 8. FILIPPI³ found that the majority had 6 arms, but 15 per cent. had 7. Those examined by HINCKS⁴ never had more than 6. Filippi considered that the difference in number was evidence that his specimens were of a species different from Claparède's. I examined many of this form at Concarneau and found six the commonest number in the free medusæ, but those still undetached frequently had 5, possibly therefore the number increases with development. [See also *Cladonema radiatum*, &c. HINCKS, *l.c.*, p. 65, &c.]

Claparède states that the 6-armed specimens had 6 radial canals, but the 8-armed usually had *four* though occasionally six, but never eight canals.

In this case note not only the frequent occurrence of Meristic Variation, but also the suggestion that particular numbers of tentacles are proper to particular localities.

- *634. Normally there is a single eye at the base of each arm. CLAPAREDE figures (*l.c.* p. 6, Pl. 1. fig. 7 α) a case of duplicity of an eye, and says that specimens occur in which each eye is doubled, so that there are two eyes at the base of each arm instead of one.
 - 635. Stomobrachium octocostatum (Æquoridæ): variety found in Cromarty Firth, ²/₃rds of size represented by FORBES (Monogr. Br. Naked-eyed Medusæ); ovaries bluish instead of orange, and without denticulated margins. Tentacles arranged in double series, long and short alternating, while in the type the series is single. The number of large tentacles same as in type. Each smaller tentacle bears vesicular body at base, without pigment or visible contents. The same variety figured by EHRENBERG, Abh. Ak. Berl., 1835, Taf. VIII. fig. 7. ROMANES, G. J., Jour. Linn. Soc. XII. p. 526. [Simultaneous Variation of the several segments.]

With Nos. 634 and 635 compare the fact that in Tiarops poly-

- ¹ Arch. f. Naturg., 1861, p. 157.
- ² Beob. üb. Anat. u. Entw. Wirbelloser Thiere, 1863, p. 5.
- ³ Mem. Ac. Torino, S. 2, xx111. p. 377.
- ⁴ Brit. Hyd. Zoophytes, 1868, p. 71.

diademata there are normally as a specific character four diadems between each pair of radial tubes, making in all sixteen instead of eight, which is the usual number in the genus. ROMANES, G. J., Jour. Linn. Soc. Zool., XII. p. 525.

*636. **Aurelia aurita.** This form exhibits an exceptional frequency of Meristic Variation. In the normal there are 16 radial canals, 4 oral lobes, 4 generative organs and 8 lithocysts. The departures from this normal form have been described in detail by EHRENBERG¹ and by ROMANES².

Meristic Variation in *Aurelia* may occur in two distinct ways, first in the degree to which there is complete separation between the generative sacs, and second in actual numerical change.

Imperfect division of generative sacs.

In the commonest form of Aurelia there are four generative organs each distinct from its neighbours, but in some specimens the generative epithelium is continuous all round the mouth, and there is then one continuous generative chamber, though opening by 4 openings as usual. (Such absence of complete separation between some of the generative organs is not rarely seen in cases of numerical Variation, v. infra.) Though the epithelium is then continuous it does not form a true circle, but is sacculated to form 4 (as normally) 3, 6, or some other number of incompletely separated parts. EIMENDERG (l. c., p. 22) saw a case in which there were 6 such sacculations, three on each side being united and having one generative pouch, but each of these pouches opened by 3 openings. There was thus a bilateral symmetry, each half containing three lobes of ovarian epithelium incompletely separated from each other. Complete union of all the generative organs was very rare.

The specimens differ greatly with regard to the degree to which the generative epithelium is folded off, and in the shapes of the generative organs. Commonly the generative epithelium is of a horse-shoe form, the two limbs of the horse-shoe not meeting each other; but in some specimens the two limbs may be to various degrees approximated, so that each generative organ is kidney-shaped or even roughly circular. (Cases figured by EMENBERG, *l. c.*, Pl. II.) [Here note the Simultaneous Variation of the single quadrants.]

Numerical Variations.

Of these the most striking and also the most frequent are variations consisting in a perfect and symmetrical change in the fundamental number of segments composing the disc. Normally there are four quadrants (Fig. 128, I). Varieties are found having only half the usual number of organs, the disc being made up of two halves, each containing one generative organ (Fig. 128, IV). Other symmetrical varieties having three, and six, as their fundamental numbers are shewn in Fig. 128, V, and II. These figures are from ROMANES. Symmetrical forms having five segments and eight segments are described and figured by EHRENBERG. As to the comparative frequency of these forms facts are given below. In each of them all the parts normally proper to one quadrant are repeated in each segment of the disc, the number of parts being greater or less than the normal in correspondence with the fundamental number of the specimen.

¹ EHRENBERG, C. G., Abh. k. Ak. Wiss., Berlin, 1835, pp. 199-202, Plates.

² ROMANES, G. J., Jour. Linn. Soc., Zool., XII. p. 528, and XIII. p. 190, Pls. xv. and xvi.

Next, the number of certain organs may vary independently of other organs. For example as seen in Fig. 128, VI the radial canal



FIG. 128. Diagrams of various forms of Aurelia aurita, slightly simplified from ROMANES. I. The normal. II. Symmetrical form with 6 radii. III. Two additional chief radial canals in opposite interradii (where manubrial lobes also were bifd) and substitution of two canals for one in another interradius. IV. Form with two generative organs. V. Form with three generative organs. VI. Symmetrical form in which the intergenital canals are all doubled, the others remaining single. VII. Apparently upper half-disc arranged as for a symmetry of four, lower half for a symmetry of six. VIII. One of the quadrants tripled (?). IX. Form resembling VI. except that in one quadrant the intergenital canal is not doubled. The descriptions are not altogether those of ROMANES.

normally lying in a plane between each pair of generative organs may in each quadrant be represented by two canals, and in correspondence with this change the number of marginal organs is proportionately changed in the quadrants affected.

But besides these changes symmetrically carried out in each quadrant or in the whole disc, one or more quadrants or a half-disc may vary *independently*. For example Fig. 128, VII, shews a specimen in which the two upper quadrants are normal but the lower half-disc is primarily divided into three. (In the case figured the parts of the lower half-disc are not quite accurately distributed). Similarly a particular quadrant may be represented by two sets of parts or by three sets (Fig. 128, VIII), the other three quadrants being normal or nearly so. I have seen a case also in which the chief symmetry was arranged as for *three* segments (having 3 oral lobes), but one of the three segments was imperfectly divided into two.

In a case of 6 segments, 3 on one side may be large and the other 3 small, somewhat as in Fig. 128, VIII, but the whole disc was not circular, the radius on the side of the large segments being the greater.

In the figures (after ROMANES) all the discs are represented as circles, but my own experience was that when there was not a truly symmetrical distribution of the generative organs the half quadrant or other segment in which the number of parts was greatest bulged outwards, thus exemplifying the general rule that when an organ divides the two resulting parts are together larger than the undivided organ.

Besides those specified, there are also irregular cases, e.g., specimens with 3 generative organs but 4 oral lobes and other parts in multiples of 4, but as EHRENBERG says in such cases it is generally possible to detect that one of the generative organs is larger than the others or even partially double. He also saw cases otherwise arranged in a symmetry of 6, but having 22 chief radial canals instead of 24, &c. Also 14 radial canals (instead of 12) were found in some cases of 3 generative organs.

As everyone will admit, it is impossible in regular threes, sixes, &c. to say that any particular segment is missing or is added rather than another.

Comparative frequency of the several forms.

*637. Among thousands of individuals seen by Ehrenberg only two were 8-rayed, 15—20 were 6-rayed, some 20—30 were 5- and 3-rayed, the remainder being 4-rayed. In percentages, 90 are 4-rayed, 3 are 3-rayed 3 are 5-rayed, 2 are 6-rayed and 2 have other numbers.

The result of an attempt to ascertain these percentages in a great shoal of *Aurelia* washed ashore on the Northumberland coast on 4 Sept. 1892 is given below. The radial canals were not counted, and the numbers apply strictly to the generative sacs only. It will be seen that the proportion of abnormals is lower than that given by Ehrenberg.

2	generative	sacs 0	
3	· · · ·	symml.: 3 oral lobes in 4 unbroken cases10	$(0.57^{\circ}/)$
3	,,	2 large, 1 small: 3 or. lobes 1	
4	,,	normal1735	
4	"	3 large, 1 small: 5 or. lobes 1	
4	,,	2 large, 2 small: 3 lobes 1	
5	"	symmetrical 5 lobes in one 2	
5	,,	not quite symmetrical 1	
6	,,	sym.: 6 lobes in 2 unbroken cases 7	$(0.39^{\circ}/)$
6	,,	not symmetrical 1	
6	,,	4 large, 2 small 1	
6	,,	4 large, 2 united: 6 lobes in 1 unbroken 2	
6	,,	3 large, 3 small: 6 lobes 1	
		1763	

There were therefore 1735 normals, 19 symmetrical varieties and 9 irregulars. It will be noted not only that the symmetrical varieties are comparatively frequent, but also that the several forms of irregularity were seen for the most part in single specimens only.

II. PEDICELLARIÆ OF ECHINODERMS.

The number of jaws in the pedicellariæ differs in different forms of Echinoderms, and I am indebted to Professor C. STEWART for information concerning them.

In Asteroidea the number of jaws is usually two, but in Luidia savignii the normal number of jaws is three.

In the Echinoidea the number of jaws is usually three, but in Asthenosoma the normal number is four.

638. Dorocidaris papillata: number of jaws in pedicellariæ



FIG. 129. Pedicellariæ of Dorocidaris papillata.
I. Normal form with three jaws.
II. A pedicellaria with four jaws from the abactinal region. (From Prof. STEWART's specimens.)

normally three as in Fig. 129, I, but occasionally four in pedicellarize of the abactinal region, as in Fig. 129, II. [Note that the variety is perfect and symmetrical.] For this fact I am obliged to Professor Stewart, who kindly allowed this figure to be made from his preparations.

- 639. Luidia ciliaris: pedicellariæ nearly all with three jaws; but on Roscoff specimens a few having two jaws occur on the borders of the ambulacral groove. In Banyul's specimens none such were found in this position, but there is one in almost all the marginal intervals. CUÉNOT, Arch. zool. exp., S. 2, V. bis, p. 18.
- 640. Asterias glacialis: occasionally three-jawed pedicellariæ like those of Luidia are found among the normal two-jawed pedicellariæ. CUÉNOT, l. c., p. 23.

MERISTIC VARIATION.

III. CELL-DIVISION.

*641. It was purposed at this point to have introduced an account of Meristic variations observed in the manner of division of nuclei and cells; but I have found that, to give adequate representation of these facts even in outline, it would be necessary not only to treat of a very complex subject with which I have no proper acquaintance, but also greatly to enlarge the scope of this work. But were no word said on these matters, indications most useful as comment on the nature of Meristic Variation at large would have to be foregone; and unwilling that these should be wholly lost I shall venture briefly to allude to so much of the matter as is needful to shew some ways in which the facts of abnormal celldivision can be used in reference to the wider question of Meristic Variation.

We have been dealing with cases of Radial repetition, and we have seen that with Variation in the number of parts the result may still be radially symmetrical. It therefore becomes of interest to note that in the case of abnormal cell-division the result of numerical change may in like manner be radially symmetrical. Cells which should normally contain two centrosomes and which should divide into two parts have been seen to contain three centro-



FIG. 130. Triasters. I. Tripolar division of nucleus in embryonic tissue of Trout (after HENNEGUY¹). II. Triaster from mammary carcinoma. Centrosomes not shewn (from FLEMMING²).

somes (Fig. 130) prior to division into three parts, and the triangle formed by the three centrosomes may be equiangular just as may be the triangle of the segments of the abnormal Aurelia (Fig. 128, V), or of the jaws of the normal pedicellaria of Dorocidaris (Fig. 129). It is, I imagine, difficult to suppose that the radial symmetry of each of these series of organs is

¹ HENNEGUY, Jour. de l'Anat. et Phys., 1891, p. 397, Pl. XIX. fig. 9. ² FLEMMING, Zellsubstanz, Kern u. Zelltheilung, 1882, Pl. VIII. fig. v. after MARTIN, Virch. Arch., 1881, LXXXVI. Pl. IV.

different in its nature, or indeed that it is anything but a visible expression of the equality of the strains tending to part each segment from its neighbours. (The case of the triaster is taken as the simplest and most plainly symmetrical, but examples of cells with greater numbers of centrosomes, sometimes dividing symmetrically, have also been seen.)

For our purpose this fact is first of use as a demonstration of the absurdity of an appeal to "Reversion" as a mode of escape from the admission that variations in Radial Symmetry may be total and perfect though the new number of segments is one which presumably never occurred in the phylogeny; for we need scarcely expect that even conspicuous defenders of the doctrine that all perfection must have been continuously evolved, will plead that the cells of every tissue in which a triaster is found did once normally divide with three poles. Yet if it be once granted that the symmetry of these abnormal forms is a sudden and new departure from the normal, it will not be easy to put the other cases on a different footing.

Though we have repudiated all concern with the causes of abnormality, mention may be made of the fact that multipolar figures, both regular and irregular, have been observed to result from the action of reagents (e.g. quinine, HERTWIG¹). Such figures are of course well known especially in the case of carcinomatous growths, and as Hertwig observes, from the resemblance of these figures to those artificially induced by chemical means it seems possible that these pathological appearances may also be the result of some chemical stimulus. But whatever be the immediate or directing causes of abnormalities in cell-division, or of those other abnormalities in the segmentation of Radial Series of larger parts, and whether any of the causes in the several cases be similar or different, we can scarcely avoid recognition that the resulting phenomena are closely alike².

¹ O. HERTWIG, Die Zelle u. d. Gewebe, 1893, pp. 192-198. ² See also a case of the presence of triasters in two bilaterally symmetrical tracts of the blastoderm of Loligo (v. infra).