EQUILIBRIUM OF ANIMAL FORM¹

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WITH TEN FIGURES

If the equilibrium of a mass be disturbed, the body will alter its position in regard to the surrounding neighborhood till it again gets into a position of equilibrium. If the form of an animal be altered through amputation of certain parts, the equilibrium of mass may or may not be altered therewith, the animal either being able to maintain its position or having to alter its posture for readjusting its equilibrium. But this is not all that may happen: it may restore its *form*, too, after some time, thus tending toward a new equilibrium of *form*, till it has reached a new stable condition.

This may involve three regulatory processes: Regeneration of lost parts from the cut surface; reduction of existing parts in contact with the cut surface; compensation at parts of the body not touched by the amputation.

The study of regeneration has long received much attention; of late reduction too has been studied more fully, especially in the lower animals, whilst compensation as a means of restoring animal form seems first to have been pointed out by me. Its study has been taken up especially in America, where Zeleny found additional cases (observed independently of my work), and Wilson, Morgan and Emmel have studied different aspects of compensatory regulation in crustaceans.

Having found the principle of compensatory regulation illustrated in the chelæ of *Alpheus*, I have been looking for other analogous cases and have found the same process in other crustaceans, especially *Callinassa* and the common Crabs, *Portunus* and

¹ Read before the International Congress of Zoology at Boston on August 22, 1907.

Carcinus, as I demonstrated at the last session of the German Naturalists' Association. It will be remembered that this compensatory regulation consists in the hypertypical growth of the smaller claw of the first pair of thoracic limbs, after autotomic removal of the big chela, whilst a hypotypical small chela regenerates. That such a "transposition" or "reversal" need not be restricted to this pair of appendages I am now able to show in *Typton spongicola* (Fig. 1), where the *second* pair of thoracic limbs is developed into asymmetrical chelæ. After removal of the bigger chela, which, by the way, may be situated normally at the right or at the left side of the body, reversal of the chelæ of this second pair is brought about (Fig. 2), the process being in all respects analogous to that in the first pair of chelæ in *Alpheus*.

But not only may the means of regeneration and compensation be clearly shown to occur in this case, but also reduction is involved to an appreciable degree, especially if the crayfish is starved during the experiment. Then each moult shows the shedding of a smaller skin and the animal is at the end of the transposition in all dimensions smaller than at the time of the operation. Thus, as in the lowest animals, a proportionate diminution of the whole form may be produced as regulation proceeds, the only difference with Morgan's "morphallaxis" lying in the bigger fragment necessary for reconstruction.

A curious instance of "compensatory reduction" was met in some experiments on cutting the nerves in crabs. As Morgan has reported, the chela generally degenerates after this operation. In a few cases, however, I was fortunate enough to get a further growth of the limb. In these the terminal joint of the big or crushing claw was removed (Fig. 3), and in one instance regenerated in a rather reduced state; but also the corresponding dactylopodite of the smaller or nipping claw lost its differentiation (Fig. 4).

Compensatory reduction may also occur in animals other than crustaceans and in other regions than in the chelæ. Męgusar, working on regeneration in beetles (Coleoptera), amputated one of the two slightly differing jaws of the *Hydrophilus* larva. Whilst there are normally two teeth on the inner side of each jaw (Fig. 5) the larva appeared after the moult succeeding the amputation

FIG. 1.

FIG. 2.

FIG. 3.

FIG. 4.

FIG. 5.

FIG. 6.

of but one jaw with but *one* tooth on the non-operated jaw, the regenerating one showing no teeth (Fig. 6).

A tendency toward a quick restoration of a symmetrical condition was also found several times in experiments of Miss Zuelzer on the regeneration and moulting periods of the isopod, *Asellus aquaticus*. When both long antennæ were removed, simultaneously, but at different levels (Fig. 7) they would be apt to appear regenerated to an *equal* length (Fig. 8) even after the next moult, though not having yet attained their normal length. In some way these conditions may be related to the different rate with which appendages regenerate from different levels.

It is not necessary that the two correlated parts be symmetrically situated. The male of the water-newt, *Triton vulgaris*, produces in its state of courtship a crest along its back and around its tail, which has a ragged appearance (Fig. 9). Kammerer cut the tail off to test the regenerative power of the secondary sexual characters. He found that at first the tail appears with smooth not ragged edges. But this is not all: the crest on the back had also lost its ragged appearance, thus conforming with the outline of the new dorsal rim of the tail (Fig. 10). It is not shed or resorbed, but keeps the height of the courtship crest.

The object of my paper is to emphasize the similarity of these processes of regeneration, reduction and compensation, in lower and higher animal forms, and their relation to the reëstablishment of the equilibrium of animal form.

FIG. 7.

FIG. 8.

FIG. 9.

FIG. 10.

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