

Panmixia.

It is now twenty years ago that I published in these columns the doctrine of Panmixia, or Cessation of Selection, and since this doctrine was independently re-enunciated by Prof. Weismann I have repeatedly had occasion both to explain and to defend our common views upon the subject. For it is surprising how many of our foremost English evolutionists seem to have found a difficulty in understanding exactly what is meant by the doctrine. In view, therefore, of Prof. Weismann's forthcoming lecture at Oxford, it seems desirable that the present standing of the matter should be presented to the consideration of English biologists. An opportunity may thus be afforded him of answering the objections which they have raised against one of the fundamental doctrines of his entire system.

In NATURE of April 12 Mr. Wallace writes:—"He (Mr. Kidd) is under the mistaken impression that the theory (*i.e.* the state) of *panmixia* leads to continuous and unlimited degeneration. Many writers have pointed out that this is an error. The amount of degeneration thus produced would be limited to that of the average of those *born* during the preceding generations in place of the average of those that had *survived*. As Prof. Lloyd Morgan puts it, the survival-mean would fall back to the birth-mean."

This way of putting it, however, was originally due to Prof. Ray Lankester, whose views and terms relating to the subject were afterwards adopted provisionally by Prof. Lloyd Morgan. It may still be remembered by your biological readers that about four years ago Prof. Ray Lankester somewhat vigorously attacked my views on the Cessation of Selection as a cause of degeneration, and disputed their identity with those of Prof. Weismann on Panmixia. He urged that by Panmixia Weismann meant, not the merely passive *cessation* of selection, but an active *reversal* of it, through Economy of Nutrition, &c.

And he strenuously maintained that a merely passive cessation of selection could not be a cause of degeneration in any degree at all. After a prolonged discussion, however, he allowed that it must be a cause of degeneration to the extent of reducing the previous "survival-mean" to the "birth-mean," but no further. In adopting this view, Prof. Lloyd Morgan estimated that "the amount of degeneration thus produced" might be set down at 5 per cent. More recently still Mr. Herbert Spencer, in the *Contemporary Review*, took the same points of exception to my Cessation of Selection as Prof. Ray Lankester had originally taken—*i.e.* that it was not the same doctrine as Weismann's Panmixia (the latter being in Mr. Spencer's understanding of it the active reversal of selection due to Economy of Nutrition, &c.), and that it could not be, in any circumstances or in any degree, a cause of degeneration.

Both these points, however, were soon settled, as far as the question of Weismann's opinion was concerned, by his replying to Mr. Spencer that the doctrine of Panmixia was identical with that of the Cessation of Selection, and also that in his opinion the principle was not merely a cause of degeneration, but, as a general rule, the *sole* cause. Moreover, he has repeatedly stated that in his opinion "the amount of degeneration thus produced" is unlimited, so that any organ which has fallen under the influence of Panmixia may, by such influence alone, be reduced to a "vestige," and finally abolished altogether. Thereupon Mr. Spencer, like his predecessors, put the question—What is there in the state of Panmixia that determines a numerical excess of *minus* over *plus* variations, such as must be supposed if the amount of degeneration due to Panmixia alone is to proceed further than the survival-mean falling to the birth-mean? Now this very pertinent question has never been answered by Prof. Weismann. He has simply taken it as self-evident, that when the maintaining influence of selection is withdrawn as regards any organ (owing to the latter having ceased to be useful) atrophy of that organ must ensue in successive generations, and this to an unlimited extent. Therefore I am unable to say what his views upon this important point may be. But in answering Mr. Spencer I gave what my own views have always been with regard to it. I hold that there are at least three very good reasons why, as soon as selection is withdrawn from an organ, the *minus* variations of that organ outnumber the *plus* variations, and therefore that it must dwindle in successive generations. These three reasons are as follows:—

(1) The survival-mean must descend to the birth-mean. This is now on all hands acknowledged. But it will only produce, at the outside, 5 per cent. of dwindling.

(2) Atavism is always at work in our domesticated varieties; and although there is no evidence to show (as is generally assumed) that but for artificial selection this would in time cause any domesticated variety to revert to its wild type, there is abundant evidence to show that the cessation of such selection is soon followed by deterioration of the artificial type—*i.e.* degeneration to a very much greater amount than can be explained by the cause above mentioned (1). And, notwithstanding that atavism in the case of specific characters is less pronounced than it is in that of domesticated varieties (owing presumably to their having been much longer inherited), still we know that even here its occurrence is neither rare nor insignificant. And it seems evident that in whatever degree it does occur in the case of any specific character, in that degree it must determine a preponderance of *minus* over *plus* variations—at any rate through 10 to 20 per cent. of degeneration. So long as the character is of use to its possessor, natural selection will suppress these atavistic (*minus*) variations. But when the character ceases to be of use, natural selection will be withdrawn as regards that character, and the resulting preponderance of *minus* variations due to atavism will lead to degeneration—more slowly, no doubt, than in the case of our domesticated productions, but still, and eventually, to some amount considerably more than that contemplated by the English naturalists who object to the doctrine of Panmixia (1). Hence, it appears to me, these naturalists must have overlooked the necessary presence of this factor under a state of Panmixia—at all events in the earlier stages of degeneration, or before atavism begins to cut both ways.

(3) As long as an organ or structure is under the influence of natural selection, any failures in the perfection of hereditary transmission will be weeded out. But as soon as natural selection ceases with regard to this organ or structure, all such imperfections will be allowed to survive, and, just as in the case of

atavistic variations, will act as a dead weight on the side of degeneration. Be it observed, degeneration may occur either in regard to size (dwindling of bulk) or to structure (disorganisation of machinery); and it is in the latter case that the present cause of degeneration under a state of Panmixia is presumably of most importance. Thus, for example, we can understand why some of the blind crustacea in dark caves should have lost their eyes, while they have not yet lost their eye-stalks. The latter, although of larger bulk than the eyes can have been, are of much less complexity in regard to structure.

These, then, are my reasons for holding that there is no "error" attaching to Weismann's theory of Panmixia as a cause of degeneration, and, so far, no one has attempted to show that there is any error attaching to these reasons. It seems to me desirable that either Mr. Wallace or some of the English naturalists who think with him should now do so, if only for the sake of seeing what Prof. Weismann may have to say upon the whole subject a week or two hence. But I write in no spirit of controversy. I merely ask for information as to what is the "error" into which both he and I are said to have fallen.

There are certain other points of comparative detail connected with the theory of Panmixia as to which, owing to his reticence, I am uncertain whether Prof. Weismann is in agreement with me. But it seems unnecessary to go into them on the present occasion. For they refer to degeneration by Panmixia below 10 to 20 per cent. of dwindling, and the importance of the doctrine lies in the fact of its destroying the direct evidence of the inherited effects of disuse on which Darwin relied in the case of domesticated animals, where, as he showed, there is no Economy of Growth or Reversal of Selection, to account for the 10 to 20 per cent. which their disused organs have undergone. Hence, one can understand why the doctrine should be obnoxious to Lamarckians, but not why such should be the case with those who disbelieve in the transmission of acquired characters. Prof. Weismann may well ask these naturalists what cause, other than Panmixia, they have to suggest whereby to supplant Darwin's explanation of these particular cases of degeneration.

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Hyères, France, April 16.