

Origin and Causes of the Sterility of first Crosses and of Hybrids.

At one time it appeared to me probable, as it has to others, that the sterility of first crosses and of hybrids might have been slowly acquired through the natural selection of slightly lessened degrees of fertility, which, like any other variation, spontaneously appeared in certain individuals of one variety when crossed with those of another variety. For it would clearly be advantageous to two varieties or incipient species if they could be kept from blending, on the same principle that, when man is selecting at the same time two varieties, it is necessary that he should keep them separate. In the first place, it may be remarked that species inhabiting distinct regions are often sterile when crossed; now it could clearly have been of no advantage to such separated species to have been rendered mutually sterile, and consequently this could not have been effected through natural selection; but it may perhaps be argued, that, if a species was rendered sterile with some one compatriot, sterility with other species would follow as a necessary contingency. In the second place, it is almost as much opposed to the theory of natural selection as to that of special creation, that in reciprocal crosses the male element of one form should have been rendered utterly impotent on a second form, while at the same time the male element of this second form is enabled freely to fertilise the first form; for this peculiar state of the reproductive system could hardly have been advantageous to either species.

In considering the probability of natural selection having come into action, in rendering species mutually sterile, the greatest difficulty will be found to lie in the existence of many graduated steps, from slightly lessened fertility to absolute sterility. It may be admitted that it would profit an incipient species, if it were rendered in some slight degree sterile when crossed with its parent form or with some other variety; for thus fewer bastardised and deteriorated offspring would be produced to commingle their blood with the new species in process of formation. But he who will take the trouble to reflect on the steps by which this first degree of sterility could be increased through natural selection to that high degree which is common with so many species, and which is universal with species which have been differentiated to a generic or family rank, will find the subject extraordinarily complex. After mature reflection, it seems to me that this could not have been effected through natural selection. Take the case of any two species which, when crossed, produced few and sterile offspring; now, what is there which could favour the survival of those individuals which happened to be endowed in a slightly higher degree with mutual infertility, and which thus approached by one small step towards absolute sterility? Yet an advance of this kind, if the theory of natural selection be brought to bear, must have incessantly occurred with many species, for a multitude are mutually quite barren. With sterile neuter insects we have reason to believe that modifications in their structure and fertility have been slowly accumulated by natural selection, from an advantage having been thus indirectly given to the community to which they belonged over other communities of the same species; but an individual animal not belonging to a social community, if rendered slightly sterile when crossed with some other variety, would not thus itself gain any advantage or indirectly give any advantage to the other individuals of the same variety, thus leading to their preservation.

But it would be superfluous to discuss this question in detail: for with plants we have conclusive evidence that the sterility of crossed species must be due to some principle, quite independent of natural selection. Both Gärtner and Kölreuter have proved that in genera including numerous species, a series can be formed from species which when crossed yield fewer and fewer seeds, to species which

never produce a single seed, but yet are affected by the pollen of certain other species, for the germen swells. It is here manifestly impossible to select the more sterile individuals, which have already ceased to yield seeds; so that this acme of sterility, when the germen alone is effected, cannot have been gained through selection; and from the laws governing the various grades of sterility being so uniform throughout the animal and vegetable kingdoms, we may infer that the cause, whatever it may be, is the same or nearly the same in all cases.

We will now look a little closer at the probable nature of the differences between species which induce sterility in first crosses and in hybrids. In the case of first crosses, the greater or less difficulty in effecting a union and in obtaining offspring apparently depends on several distinct causes. There must sometimes be a physical impossibility in the male element reaching the ovule, as would be the case with a plant having a pistil too long for the pollen-tubes to reach the ovarium. It has also been observed that when the pollen of one species is placed on the stigma of a distantly allied species, though the pollen-tubes protrude, they do not penetrate the stigmatic surface. Again, the male element may reach the female element, but be incapable of causing an embryo to be developed, as seems to have been the case with some of Thuret's experiments on Fuci. No explanation can be given of these facts, any more than why certain trees cannot be grafted on others. Lastly, an embryo may be developed, and then perish at an early period. This latter alternative has not been sufficiently attended to; but I believe, from observations communicated to me by Mr. Hewitt, who has had great experience in hybridising pheasants and fowls, that the early death of the embryo is a very frequent cause of sterility in first crosses. Mr. Salter has recently given the results of an examination of about 500 eggs produced from various crosses between three species of Gallus and their hybrids; the majority of these eggs had been fertilised; and in the majority of the fertilised eggs, the embryos had either been partially developed and had then perished, or had become nearly mature, but the young chickens had been unable to break through the shell. Of the chickens which were born, more than four-fifths died within the first few days, or at latest weeks, "without any obvious cause, apparently from mere inability to live;" so that from the 500 eggs only twelve chickens were reared. With plants, hybridized embryos probably often perish in a like manner; at least it is known that hybrids raised from very distinct species are sometimes weak and dwarfed, and perish at an early age; of which fact Max Wichura has recently given some striking cases with hybrid willows. It may be here worth noticing that in some cases of parthenogenesis, the embryos within the eggs of silk moths which had not been fertilised, pass through their early stages of development and then perish like the embryos produced by a cross between distinct species. Until becoming acquainted with these facts, I was unwilling to believe in the frequent early death of hybrid embryos; for hybrids, when once born, are generally healthy and long-lived, as we see in the case of the common mule. Hybrids, however, are differently circumstanced before and after birth: when born and living in a country where their two parents live, they are generally placed under suitable conditions of life. But a hybrid partakes of only half of the nature and constitution of its mother; it may therefore, before birth, as long as it is nourished within its mother's womb, or within the egg or seed produced by the mother, be exposed to conditions in some degree unsuitable, and consequently be liable to perish at an early period; more especially as all very young beings are eminently sensitive to injurious or unnatural conditions of life. But after all, the cause more probably lies in some imperfection in the original act of impregnation, causing the embryo to be imperfectly developed, rather than in the conditions to which it is subsequently exposed.

In regard to the sterility of hybrids, in which the sexual elements are imperfectly developed, the case is somewhat different. I have more than once alluded to a large body of facts showing that, when animals and plants are removed from their natural conditions, they are extremely liable to have their reproductive systems seriously affected. This, in fact, is the great bar to the domestication of animals.

Between the sterility thus superinduced and that of hybrids, there are many points of similarity. In both cases the sterility is independent of general health, and is often accompanied by excess of size or great luxuriance. In both cases the sterility occurs in various degrees; in both, the male element is the most liable to be affected; but sometimes the female more than the male. In both, the tendency goes to a certain extent with systematic affinity, for whole groups of animals and plants are rendered impotent by the same unnatural conditions; and whole groups of species tend to produce sterile hybrids. On the other hand, one species in a group will sometimes resist great changes of conditions with unimpaired fertility; and certain species in a group will produce unusually fertile hybrids. No one can tell till he tries, whether any particular animal will breed under confinement, or any exotic plant seed freely under culture; nor can he tell till he tries, whether any two species of a genus will produce more or less sterile hybrids. Lastly, when organic beings are placed during several generations under conditions not natural to them, they are extremely liable to vary, which seems to be partly due to their reproductive systems having been specially affected, though in a lesser degree than when sterility ensues. So it is with hybrids, for their offspring in successive generations are eminently liable to vary, as every experimentalist has observed.

Thus we see that when organic beings are placed under new and unnatural conditions, and when hybrids are produced by the unnatural crossing of two species, the reproductive system, independently of the general state of health, is affected in a very similar manner. In the one case, the conditions of life have been disturbed, though often in so slight a degree as to be inappreciable by us; in the other case, or that of hybrids, the external conditions have remained the same, but the organisation has been disturbed by two distinct structures and constitutions, including of course the reproductive systems, having been blended into one. For it is scarcely possible that two organisations should be compounded into one, without some disturbance occurring in the development, or periodical action, or mutual relations of the different parts and organs one to another or to the conditions of life. When hybrids are able to breed inter se, they transmit to their offspring from generation to generation the same compounded organisation, and hence we need not be surprised that their sterility, though in some degree variable, does not diminish; it is even apt to increase, this being generally the result, as before explained, of too close interbreeding. The above view of the sterility of hybrids being caused by two constitutions being compounded into one has been strongly maintained by Max Wichura.

It must, however, be owned that we cannot understand, on the above or any other view, several facts with respect to the sterility of hybrids; for instance, the unequal fertility of hybrids produced from reciprocal crosses; or the increased sterility in those hybrids which occasionally and exceptionally resemble closely either pure parent. Nor do I pretend that the foregoing remarks go to the root of the matter: no explanation is offered why an organism, when placed under unnatural conditions, is rendered sterile. All that I have attempted to show is, that in two cases, in some respects allied, sterility is the common result,— in the one case from the conditions of life having been disturbed, in the other case from the organisation having been disturbed by two organisations being compounded into one.

A similar parallelism holds good with an allied yet very different class of facts. It is an old and almost universal belief, founded on a considerable body of evidence, which I have elsewhere given, that slight changes in the conditions of life are beneficial to all living things. We see this acted on by farmers and gardeners in their frequent exchanges of seed, tubers, &c., from one soil or climate to another, and back again. During the convalescence of animals, great benefit is derived from almost any change in their habits of life. Again, both with plants and animals, there is the clearest evidence that a cross between individuals of the same species, which differ to a certain extent, gives vigour and fertility to the offspring; and that close interbreeding continued during several generations between the nearest

relations, if these be kept under the same conditions of life, almost always leads to decreased size, weakness, or sterility.

Hence it seems that, on the one hand, slight changes in the conditions of life benefit all organic beings, and on the other hand, that slight crosses, that is, crosses between the males and females of the same species, which have been subjected to slightly different conditions, or which have slightly varied, give vigour and fertility to the offspring. But, as we have seen, organic beings long habituated to certain uniform conditions under a state of nature, when subjected, as under confinement, to a considerable change in their conditions, very frequently are rendered more or less sterile; and we know that a cross between two forms that have become widely or specifically different, produce hybrids which are almost always in some degree sterile. I am fully persuaded that this double parallelism is by no means an accident or an illusion. He who is able to explain why the elephant, and a multitude of other animals, are incapable of breeding when kept under only partial confinement in their native country, will be able to explain the primary cause of hybrids being so generally sterile. He will at the same time be able to explain how it is that the races of some of our domesticated animals, which have often been subjected to new and not uniform conditions, are quite fertile together, although they are descended from distinct species, which would probably have been sterile if aboriginally crossed. The above two parallel series of facts seem to be connected together by some common but unknown bond, which is essentially related to the principle of life; this principle, according to Mr. Herbert Spencer, being that life depends on, or consists in, the incessant action and reaction of various forces, which, as throughout nature, are always tending towards an equilibrium; and when this tendency is slightly disturbed by any change, the vital forces gain in power.

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