

## CHAPTER XVII.

ON THE GOOD EFFECTS OF CROSSING, AND ON THE EVIL EFFECTS  
OF CLOSE INTERBREEDING.

DEFINITION OF CLOSE INTERBREEDING—AUGMENTATION OF MORBID TENDENCIES—GENERAL EVIDENCE OF THE GOOD EFFECTS DERIVED FROM CROSSING, AND ON THE EVIL EFFECTS FROM CLOSE INTERBREEDING—CATTLE, CLOSELY INTERBRED; HALF-WILD CATTLE LONG KEPT IN THE SAME PARKS—SHEEP—FALLOW-DEER—DOGS, RABBITS, PIGS—MAN, ORIGIN OF HIS ABHORRENCE OF INCESTUOUS MARRIAGES—FOWLS—PIGEONS—HIVE-BEES—PLANTS, GENERAL CONSIDERATIONS ON THE BENEFITS DERIVED FROM CROSSING—MELONS, FRUIT-TREES, PEAS, CABBAGES, WHEAT, AND FOREST-TREES—ON THE INCREASED SIZE OF HYBRID PLANTS, NOT EXCLUSIVELY DUE TO THEIR STERILITY—ON CERTAIN PLANTS WHICH EITHER NORMALLY OR ABNORMALLY ARE SELF-IMPOTENT, BUT ARE FERTILE, BOTH ON THE MALE AND FEMALE SIDE, WHEN CROSSED WITH DISTINCT INDIVIDUALS EITHER OF THE SAME OR ANOTHER SPECIES—CONCLUSION.

THE gain in constitutional vigour, derived from an occasional cross between individuals of the same variety, but belonging to distinct families, or between distinct varieties, has not been so largely or so frequently discussed, as have the evil effects of too close interbreeding. But the former point is the more important of the two, inasmuch as the evidence is more decisive. The evil results from close interbreeding are difficult to detect, for they accumulate slowly, and differ much in degree with different species; whilst the good effects which almost invariably follow a cross are from the first manifest. It should, however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour. In relation to the subject of domestication, the whole question is of some importance, as too close interbreeding interferes with the improvement of old races. It is important as indirectly bearing on Hybridism; and possibly on the extinction of species, when any form has become so rare that only a few individuals remain within a confined area. It bears in an

important manner on the influence of free intercrossing, in obliterating individual differences, and thus giving uniformity of character to the individuals of the same race or species; for if additional vigour and fertility be thus gained, the crossed offspring will multiply and prevail, and the ultimate result will be far greater than otherwise would have occurred. Lastly, the question is of high interest, as bearing on mankind. I shall therefore discuss this subject at full length. As the facts which prove the evil effects of close interbreeding are more copious, though less decisive, than those on the good effects of crossing, I shall, under each group of beings, begin with the former.

There is no difficulty in defining what is meant by a cross; but this is by no means easy in regard to "breeding in and in" or "too close interbreeding," because, as we shall see, different species of animals are differently affected by the same degree of interbreeding. The pairing of a father and daughter, or mother and son, or brothers and sisters, if carried on during several generations, is the closest possible form of interbreeding. But some good judges, for instance Sir J. Sebright, believe that the pairing of a brother and sister is much closer than that of parents and children; for when the father is matched with his daughter he crosses, as is said, with only half his own blood. The consequences of close interbreeding carried on for too long a time, are, as is generally believed, loss of size, constitutional vigour, and fertility, sometimes accompanied by a tendency to malformation. Manifest evil does not usually follow from pairing the nearest relations for two, three, or even four generations; but several causes interfere with our detecting the evil—such as the deterioration being very gradual, and the difficulty of distinguishing between such direct evil and the inevitable augmentation of any morbid tendencies which may be latent or apparent in the related parents. On the other hand, the benefit from a cross, even when there has not been any very close interbreeding, is almost invariably at once conspicuous. There is good reason to believe, and this was the opinion of that most experienced observer Sir J. Sebright,<sup>1</sup> that the evil

<sup>1</sup> 'The Art of Improving the Breed, &c.,' 1809, p. 16.

effects of close interbreeding may be checked or quite prevented by the related individuals being separated for a few generations and exposed to different conditions of life. This conclusion is now held by many breeders; for instance Mr. Carr<sup>2</sup> remarks, it is a well-known "fact that a change of soil and climate effects perhaps almost as great a change in the constitution as would result from an infusion of fresh blood." I hope to show in a future work that consanguinity by itself counts for nothing, but acts solely from related organisms generally having a similar constitution, and having been exposed in most cases to similar conditions.

That any evil directly follows from the closest interbreeding has been denied by many persons; but rarely by any practical breeder; and never, as far as I know, by one who has largely bred animals which propagate their kind quickly. Many physiologists attribute the evil exclusively to the combination and consequent increase of morbid tendencies common to both parents; and that this is an active source of mischief there can be no doubt. It is unfortunately too notorious that men and various domestic animals endowed with a wretched constitution, and with a strong hereditary disposition to disease, if not actually ill, are fully capable of procreating their kind. Close interbreeding, on the other hand, often induces sterility; and this indicates something quite distinct from the augmentation of morbid tendencies common to both parents. The evidence immediately to be given convinces me that it is a great law of nature, that all organic beings profit from an occasional cross with individuals not closely related to them in blood; and that, on the other hand, long-continued close interbreeding is injurious.

Various general considerations have had much influence in leading me to this conclusion; but the reader will probably rely more on special facts and opinions. The authority of experienced observers, even when they do not advance the grounds of their belief, is of some little value. Now almost all men who have bred many kinds of animals and have written on the subject, such as Sir J. Sebright, Andrew

\* 'The History of the Rise and Progress of the Killerby, &c. Herds,' p. 41.

Knight, &c.,<sup>3</sup> have expressed the strongest conviction on the impossibility of long-continued close interbreeding. Those who have compiled works on agriculture, and have associated much with breeders, such as the sagacious Youatt, Low, &c., have strongly declared their opinion to the same effect. Prosper Lucas, trusting largely to French authorities, has come to a similar conclusion. The distinguished German agriculturist Hermann von Nathusius, who has written the most able treatise on this subject which I have met with, concurs; and as I shall have to quote from this treatise, I may state that Nathusius is not only intimately acquainted with works on agriculture in all languages, and knows the pedigrees of our British breeds better than most Englishmen, but has imported many of our improved animals, and is himself an experienced breeder.

Evidence of the evil effects of close interbreeding can most readily be acquired in the case of animals, such as fowls, pigeons, &c., which propagate quickly, and, from being kept in the same place, are exposed to the same conditions. Now I have inquired of very many breeders of these birds, and I have hitherto not met with a single man who was not thoroughly convinced that an occasional cross with another strain of the same sub-variety was absolutely necessary. Most breeders of highly improved or fancy birds value their own strain, and are most unwilling, at the risk, in their opinion, of deterioration, to make a cross. The purchase of a first-rate bird of another strain is expensive, and exchanges are troublesome; yet all breeders, as far as I can hear, excepting those who keep large stocks at different places for the sake of crossing, are driven after a time to take this step.

Another general consideration which has had great influence on my mind is, that with all hermaphrodite animals and plants, which it might have been thought would have perpetually fertilised themselves and been thus subjected for long ages to the closest interbreeding, there is not a single species, as far as I can discover, in which the structure ensures self-fertilisation. On the contrary, there are in a multitude of

<sup>3</sup> For Andrew Knight, see A. 227. Sir J. Sebright's Treatise has Walker, on 'Intermarriage,' 1838, p. just been quoted.

cases, as briefly stated in the fifteenth chapter, manifest adaptations which favour or inevitably lead to an occasional cross between one hermaphrodite and another of the same species; and these adaptive structures are utterly purposeless, as far as we can see, for any other end.

With *Cattle* there can be no doubt that extremely close interbreeding may be long carried on advantageously with respect to external characters, and with no manifest evil as far as constitution is concerned. The case of Bakewell's Longhorns, which were closely interbred for a long period, has often been quoted; yet Youatt says<sup>4</sup> the breed "had acquired a delicacy of constitution inconsistent with common management," and "the propagation of the species was not always certain." But the Shorthorns offer the most striking case of close interbreeding; for instance, the famous bull Favourite (who was himself the offspring of a half-brother and sister from Foljambe) was matched with his own daughter, granddaughter, and great-granddaughter; so that the produce of this last union, or the great-great-granddaughter, had 15-16ths, or 93·75 per cent. of the blood of Favourite in her veins. This cow was matched with the bull Wellington, having 62·5 per cent. of Favourite blood in his veins, and produced Clarissa; Clarissa was matched with the bull Lancaster, having 68·75 of the same blood, and she yielded valuable offspring.<sup>5</sup> Nevertheless Collings, who reared these animals, and was a strong advocate for close breeding, once crossed his stock with a Galloway, and the cows from this cross realised the highest prices. Bates's herd was esteemed the most celebrated in the world. For thirteen years he bred most closely in and in; but during the next seventeen years, though he had the most exalted notion of the value of his own stock, he thrice infused fresh blood into his herd: it is said that he did this, not to improve the form of his animals, but on account of their lessened fertility. Mr. Bates's own view, as given by a celebrated breeder,<sup>6</sup>

<sup>4</sup> 'Cattle,' p. 199.

<sup>5</sup> I give this on the authority of Nathusius, 'Ueber Shorthorn Rindvieh,' 1857, s. 71 (see also 'Gardener's Chronicle,' 1860, p. 270). But Mr. J. Storer, a large breeder of cattle, informs me that the parentage of Clarissa is not well authenticated. In the first vol. of the 'Herd Book,' she was entered as having six descents from Favourite, "which was a palpable mistake," and in all subsequent editions she was spoken of as having only four descents. Mr. Storer doubts even about the four, as no names of

the dams are given. Moreover, Clarissa bore "only two bulls and one heifer, and in the next generation her progeny became extinct." Analogous cases of close interbreeding are given in a pamphlet published by Mr. C. Macknight and Dr. H. Madden, 'On the True Principles of Breeding;' Melbourne, Australia, 1865.

<sup>6</sup> Mr. Willoughby Wood, in 'Gardener's Chronicle,' 1855, p. 411; and 1860, p. 270. See the very clear tables and pedigrees given in Nathusius' 'Rindvieh,' s. 72-77.

was, that "to breed in-and-in from a bad stock was ruin and devastation; yet that the practice may be safely followed within certain limits when the parents so related are descended from first-rate animals." We thus see that there has been much close interbreeding with Shorthorns; but Nathusius, after the most careful study of their pedigrees, says that he can find no instance of a breeder who has strictly followed this practice during his whole life. From this study and his own experience, he concludes that close interbreeding is necessary to ennoble the stock; but that in effecting this the greatest care is necessary, on account of the tendency to infertility and weakness. It may be added, that another high authority<sup>7</sup> asserts that many more calves are born cripples from Shorthorns than from other and less closely interbred races of cattle.

Although by carefully selecting the best animals (as Nature effectually does by the law of battle) close interbreeding may be long carried on with cattle, yet the good effects of a cross between almost any two breeds is at once shown by the greater size and vigour of the offspring; as Mr. Spooner writes to me, "crossing distinct breeds certainly improves cattle for the butcher." Such crossed animals are of course of no value to the breeder; but they have been raised during many years in several parts of England to be slaughtered;<sup>8</sup> and their merit is now so fully recognised, that at fat-cattle shows a separate class has been formed for their reception. The best fat ox at the great show at Islington in 1862 was a crossed animal.

The half-wild cattle, which have been kept in British parks probably for 400 or 500 years, or even for a longer period, have been advanced by Culley and others as a case of long-continued interbreeding within the limits of the same herd without any consequent injury. With respect to the cattle at Chillingham, the late Lord Tankerville owned that they were bad breeders.<sup>9</sup> The agent, Mr. Hardy, estimates (in a letter to me, dated May, 1861) that in the herd of about fifty the average number annually slaughtered, killed by fighting, and dying, is about ten, or one in five. As the herd is kept up to nearly the same average number, the annual rate of increase must be likewise about one in five. The bulls, I may add, engage in furious battles, of which battles the present Lord Tankerville has given me a graphic description, so that there will always be rigorous selection of the most vigorous males. I procured in 1855 from Mr. D. Gardner, agent to the Duke of Hamilton,

<sup>7</sup> Mr. Wright, 'Journal of Royal Agricult. Soc.,' vol. vii., 1846, p. 204. Mr. J. Downing (a successful breeder of Shorthorns in Ireland) informs me that the raisers of the great families of Shorthorns carefully conceal their sterility and want of constitution. He adds that Mr. Bates, after he had

bred his herd in-and-in for some years, "lost in one season twenty-eight calves solely from want of constitution."

<sup>8</sup> Youatt on Cattle, p. 202.

<sup>9</sup> 'Report British Assoc., Zoolog. Sect.,' 1838.

the following account of the wild cattle kept in the Duke's park in Lanarkshire, which is about 200 acres in extent. The number of cattle varies from sixty-five to eighty; and the number annually killed (I presume by all causes) is from eight to ten; so that the annual rate of increase can hardly be more than one in six. Now in South America, where the herds are half-wild, and therefore offer a nearly fair standard of comparison, according to Azara the natural increase of the cattle on an estancia is from one-third to one-fourth of the total number, or one in between three and four and this, no doubt, applies exclusively to adult animals fit for consumption. Hence the half-wild British cattle which have long interbred within the limits of the same herd are relatively far less fertile. Although in an unenclosed country like Paraguay there must be some crossing between the different herds, yet even there the inhabitants believe that the occasional introduction of animals from distant localities is necessary to prevent "degeneration in size and diminution of fertility."<sup>10</sup> The decrease in size from ancient times in the Chillingham and Hamilton cattle must have been prodigious, for Professor Rüttimeyer has shown that they are almost certainly the descendants of the gigantic *Bos primigenius*. No doubt this decrease in size may be largely attributed to less favourable conditions of life; yet animals roaming over large parks, and fed during severe winters, can hardly be considered as placed under very unfavourable conditions.

With *Sheep* there has often been long-continued interbreeding within the limits of the same flock; but whether the nearest relations have been matched so frequently as in the case of Shorthorn cattle, I do not know. The Messrs. Brown during fifty years have never infused fresh blood into their excellent flock of Leicesters. Since 1810 Mr. Barford has acted on the same principle with the Foscoote flock. He asserts that half a century of experience has convinced him that when two nearly related animals are quite sound in constitution, in-and-in breeding does not induce degeneracy; but he adds that he "does not pride himself on breeding from the nearest affinities." In France the Naz flock has been bred for sixty years without the introduction of a single strange ram.<sup>11</sup> Nevertheless, most great breeders of sheep have protested against close interbreeding prolonged for too great a length of time.<sup>12</sup> The most celebrated of recent breeders, Jonas Webb, kept five separate families to work on, thus "retaining the requisite distance of relationship between the sexes;"<sup>13</sup> and what is probably of greater importance, the separate flocks will have been exposed to somewhat different conditions.

<sup>10</sup> Azara, 'Quadrupèdes du Paraguay,' tom. ii. pp. 354, 368.

<sup>11</sup> For the case of the Messrs. Brown, see 'Gard. Chronicle,' 1855, p. 26. For the Foscoote flock, 'Gard. Chron.,' 1860, p. 416. For the Naz

flock, 'Bull. de la Soc. d'Acclimat.,' 1860, p. 477.

<sup>12</sup> Nathusius, 'Rindvieh,' s. 65; Youatt on Sheep, p. 495.

<sup>13</sup> 'Gard. Chronicle,' 1861, p. 631.

Although by the aid of careful selection the near interbreeding of sheep may be long continued without any manifest evil, yet it has often been the practice with farmers to cross distinct breeds to obtain animals for the butcher, which plainly shows that good of some kind is derived from this practice. We have excellent evidence on this head from Mr. S. Druce,<sup>14</sup> who gives in detail the comparative numbers of four pure breeds and of a cross-breed which can be supported on the same ground, and he gives their produce in fleece and carcase. A high authority, Mr. Pusey, sums up the result in money value during an equal length of time, namely (neglecting shillings), for Cotswolds 248*l.*, for Leicesters 223*l.*, for Southdowns 204*l.*, for Hampshire Downs 264*l.*, and for the cross-bred 293*l.* A former celebrated breeder, Lord Somerville, states that his half-breeds from Ryelands and Spanish sheep were larger animals than either the pure Ryelands or pure Spanish sheep. Mr. Spooner concludes his excellent Essay on Crossing by asserting that there is a pecuniary advantage in judicious cross-breeding, especially when the male is larger than the female.<sup>15</sup>

As some of our British parks are ancient, it occurred to me that there must have been long-continued close interbreeding with the fallow-deer (*Cervus dama*) kept in them; but on inquiry I find that it is a common practice to infuse new blood by procuring bucks from other parks. Mr. Shirley,<sup>16</sup> who has carefully studied the management of deer, admits that in some parks there has been no admixture of foreign blood from a time beyond the memory of man. But he concludes "that in the end the constant breeding in-and-in is sure to tell to the disadvantage of the whole herd, though it may take a very long time to prove it; moreover, when we find, as is very constantly the case, that the introduction of fresh blood has been of the very greatest use to deer, both by improving their size and appearance, and particularly by being of service in removing the taint of 'rickback,' if not of other diseases, to which deer are sometimes subject when the blood has not been changed, there can, I think, be no doubt but that a judicious cross with a good stock is of the greatest consequence, and is indeed essential, sooner or later, to the prosperity of every well-ordered park."

Mr. Meynell's famous foxhounds have been adduced, as showing that no ill effects follow from close interbreeding; and Sir J. Sebright ascertained from him that he frequently bred from father and daughter, mother and son, and sometimes even from brothers and sisters. With greyhounds also there has been much close interbreeding, but the best breeders agree that it may be carried

<sup>14</sup> 'Journal R. Agricult. Soc.,' vol. xiv., 1853, p. 212.

<sup>15</sup> Lord Somerville, 'Facts on Sheep and Husbandry,' p. 6. Mr. Spooner, in 'Journal of Royal Agricult. Soc. of England,' vol. xx. part

ii. See also an excellent paper on the same subject in 'Gard. Chronicle,' 1860, p. 321, by Mr. Charles Howard.

<sup>16</sup> 'Some Account of English Deer Parks,' by Evelyn P. Shirley, 1867.



too far.<sup>17</sup> But Sir J. Sebright, declares,<sup>18</sup> that by breeding *in-and-in*, by which he means matching brothers and sisters, he has actually seen the offspring of strong spaniels degenerate into weak and diminutive lapdogs. The Rev. W. D. Fox has communicated to me the case of a small lot of bloodhounds, long kept in the same family, which had become very bad breeders, and nearly all had a bony enlargement in the tail. A single cross with a distinct strain of bloodhounds restored their fertility, and drove away the tendency to malformation in the tail. I have heard the particulars of another case with bloodhounds, in which the female had to be held to the male. Considering how rapid is the natural increase of the dog, it is difficult to understand the large price of all highly improved breeds, which almost implies long-continued close interbreeding, except on the belief that this process lessens fertility and increases liability to distemper and other diseases. A high authority, Mr. Scrope, attributes the rarity and deterioration in size of the Scotch deerhound (the few individuals formerly existing throughout the country being all related) in large part to close interbreeding.

With all highly-bred animals there is more or less difficulty in getting them to procreate quickly, and all suffer much from delicacy of constitution. A great judge of rabbits<sup>19</sup> says, "the long-eared does are often too highly bred or forced in their youth to be of much value as breeders, often turning out barren or bad mothers." They often desert their young, so that it is necessary to have nurse-rabbits, but I do not pretend to attribute all these evil results to close interbreeding.<sup>20</sup>

With respect to *Pigs* there is more unanimity amongst breeders on the evil effects of close interbreeding than, perhaps, with any other large animal. Mr. Druce, a great and successful breeder of the Improved Oxfordshires (a crossed race), writes, "without a change of boars of a different tribe, but of the same breed, constitution cannot be preserved." Mr. Fisher Hobbs, the raiser of the

<sup>17</sup> Stonehenge, 'The Dog,' 1867, pp. 175-188.

<sup>18</sup> 'The Art of Improving the Breed,' &c., p. 13. With respect to Scotch deerhounds, see Scrope's 'Art of Deer Stalking,' pp. 350-353.

<sup>19</sup> 'Cottage Gardener,' 1861, p. 327.

<sup>20</sup> Mr. Huth gives ('The Marriage of Near Kin,' 1875, p. 302) from the 'Bulletin de l'Acad. R. de Méd. de Belgique' (vol. ix., 1866, pp. 287, 305), several statements made by a M. Legrain with respect to crossing brother and sister rabbits for five or six successive generations with no consequent evil results. I was so much surprised at this account, and

at M. Legrain's invariable success in his experiments, that I wrote to a distinguished naturalist in Belgium to inquire whether M. Legrain was a trustworthy observer. In answer, I have heard that, as doubts were expressed about the authenticity of these experiments, a commission of inquiry was appointed, and that at a succeeding meeting of the Society ('Bull. de l'Acad. R. de Méd. de Belgique,' 1867, 3rd series, Tome 1, No. 1 to 5), Dr. Crocq reported "qu'il était matériellement impossible que M. Legrain ait fait les expériences qu'il annonce." To this public accusation no satisfactory answer was made.

celebrated Improved Essex breed, divided his stock into three separate families, by which means he maintained the breed for more than twenty years, "by judicious selection from the *three distinct families*."<sup>21</sup> Lord Western was the first importer of a Neapolitan boar and sow. "From this pair he bred in-and-in, until the breed was in danger of becoming extinct, a sure result (as Mr. Sidney remarks) of in-and-in breeding." Lord Western then crossed his Neapolitan pigs with the old Essex, and made the first great step towards the Improved Essex breed. Here is a more interesting case. Mr. J. Wright, well known as a breeder, crossed<sup>22</sup> the same boar with the daughter, granddaughter, and great-granddaughter, and so on for seven generations. The result was, that in many instances the offspring failed to breed; in others they produced few that lived; and of the latter many were idiotic, without sense, even to suck, and when attempting to move could not walk straight. Now it deserves especial notice, that the two last sows produced by this long course of interbreeding were sent to other boars, and they bore several litters of healthy pigs. The best sow in external appearance produced during the whole seven generations was one in the last stage of descent; but the litter consisted of this one sow. She would not breed to her sire, yet bred at the first trial to a stranger in blood. So that, in Mr. Wright's case, long-continued and extremely close interbreeding did not affect the external form or merit of the young; but with many of them the general constitution and mental powers, and especially the reproductive functions, were seriously affected.

Nathusius gives<sup>23</sup> an analogous and even more striking case: he imported from England a pregnant sow of the large Yorkshire breed, and bred the product closely in-and-in for three generations: the result was unfavourable, as the young were weak in constitution, with impaired fertility. One of the latest sows, which he esteemed a good animal, produced, when paired with her own uncle (who was known to be productive with sows of other breeds), a litter of six, and a second time a litter of only five weak young pigs. He then paired this sow with a boar of a small black breed, which he had likewise imported from England; this boar, when matched with sows of his own breed, produced from seven to nine young. Now, the sow of the large breed, which was so unproductive when paired with her own uncle, yielded to the small black boar, in the first litter twenty-one, and in the second litter eighteen young pigs; so that in one year she produced thirty-nine fine young animals!

As in the case of several other animals already mentioned, even

<sup>21</sup> Sidney's edit. of 'Youatt on the Pig,' 1860, p. 30; p. 33, quotation from Mr. Druce; p. 29, on Lord Western's case.

<sup>22</sup> 'Journal of Royal Agricult. Soc. of England,' 1846, vol. vii. p. 205.

<sup>23</sup> 'Ueber Rindvieh,' &c., s. 78.

Col. Le Couteur, who has done so much for the agriculture of Jersey, writes to me that from possessing a fine breed of pigs he bred them very closely, twice pairing brothers and sisters, but nearly all the young had fits and died suddenly.

when no injury is perceptible from moderately close interbreeding, yet, to quote the words of Mr. Coate (who five times won the annual gold medal of the Smithfield Club Show for the best pen of pigs), "Crosses answer well for profit to the farmer, as you get more constitution and quicker growth; but for me, who sell a great number of pigs for breeding purposes, I find it will not do, as it requires many years to get anything like purity of blood again."<sup>24</sup>

Almost all the animals as yet mentioned are gregarious, and the males must frequently pair with their own daughters, for they expel the young males as well as all intruders, until forced by old age and loss of strength to yield to some stronger male. It is therefore not improbable that gregarious animals may have been rendered less susceptible than non-social species to the evil consequences of close interbreeding, so that they may be enabled to live in herds without injury to their offspring. Unfortunately we do not know whether an animal like the cat, which is not gregarious, would suffer from close interbreeding in a greater degree than our other domesticated animals. But the pig is not, as far as I can discover, strictly gregarious, and we have seen that it appears eminently liable to the evil effects of close interbreeding. Mr. Huth, in the case of the pig, attributes (p. 285) these effects to their having been "cultivated most for their fat," or to the selected individuals having had a weak constitution; but we must remember that it is great breeders who have brought forward the above cases, and who are far more familiar than ordinary men can be, with the causes which are likely to interfere with the fertility of their animals.

The effects of close interbreeding in the case of man is a difficult subject, on which I will say but little. It has been discussed by various authors under many points of view.<sup>25</sup>

<sup>24</sup> Sidney on the Pig, p. 36. See also note, p. 34. Also Richardson on the Pig, 1847, p. 26.

<sup>25</sup> Dr. Dally has published an excellent article (translated in the 'Anthropolog. Review,' May, 1864, p. 65), criticising all writers who have maintained that evil follows from consanguineous marriages. No doubt on this side of the question many advo-

cates have injured their cause by inaccuracies: thus it has been stated (Devay, 'Du Danger des Mariages,' &c., 1862, p. 141) that the marriages of cousins have been prohibited by the legislature of Ohio; but I have been assured, in answer to inquiries made in the United States, that this statement is a mere fable.

Mr. Tylor<sup>26</sup> has shown that with widely different races in the most distant quarters of the world, marriages between relations—even between distant relations—have been strictly prohibited. There are, however, many exceptions to the rule, which are fully given by Mr. Huth.<sup>27</sup> It is a curious problem how these prohibitions arose during early and barbarous times. Mr. Tylor is inclined to attribute them to the evil effects of consanguineous marriages having been observed; and he ingeniously attempts to explain some apparent anomalies in the prohibition not extending equally to the relations on the male and female side. He admits, however, that other causes, such as the extension of friendly alliances, may have come into play. Mr. W. Adam, on the other hand, concludes that related marriages are prohibited and viewed with repugnance, from the confusion which would thus arise in the descent of property, and from other still more recondite reasons. But I cannot accept these views, seeing that incest is held in abhorrence by savages such as those of Australia and South America,<sup>28</sup> who have no property to bequeath, or fine moral feelings to confuse, and who are not likely to reflect on distant evils to their progeny. According to Mr. Huth the feeling is the indirect result of exogamy, inasmuch as when this practice ceased in any tribe and it became endogamous, so that marriages were strictly confined to the same tribe, it is not unlikely that a vestige of the former practice would still be retained, so that closely-related marriages would be prohibited. With respect to exogamy itself Mr. MacLennan believes that it arose from a scarcity of women, owing to female infanticide, aided perhaps by other causes.

It has been clearly shown by Mr. Huth that there is no

<sup>26</sup> See his interesting work on the 'Early History of Man,' 1865, chap. x.

<sup>27</sup> 'The Marriage of Near Kin,' 1875. The evidence given by Mr. Huth would, I think, have been even more valuable than it is on this and some other points, if he had referred solely to the works of men who had long resided in each country referred to, and who showed that they possessed

judgment and caution. See also Mr. W. Adam, 'On Consanguinity in Marriage' in the 'Fortnightly Review,' 1855, p. 710. Also Hofacker, 'Ueber die Eigenschaften,' &c., 18:8.

<sup>28</sup> Sir G. Grey's 'Journal of Expeditions into Australia,' vol. ii. p. 243; and Dobrizhoffer, 'On the Abipones of South America.'

instinctive feeling in man against incest any more than in gregarious animals. We know also how readily any prejudice or feeling may rise to abhorrence, as shown by Hindus in regard to objects causing defilement. Although there seems to be no strong inherited feeling in mankind against incest, it seems possible that men during primeval times may have been more excited by strange females than by those with whom they habitually lived; in the same manner as according to Mr. Cupples,<sup>29</sup> male deerhounds are inclined towards strange females, while the females prefer dogs with whom they have associated. If any such feeling formerly existed in man, this would have led to a preference for marriages beyond the nearest kin, and might have been strengthened by the offspring of such marriages surviving in greater numbers, as analogy would lead us to believe would have occurred.

Whether consanguineous marriages, such as are permitted in civilised nations, and which would not be considered as close interbreeding in the case of our domesticated animals, cause any injury will never be known with certainty until a census is taken with this object in view. My son, George Darwin, has done what is possible at present by a statistical investigation,<sup>30</sup> and he has come to the conclusion, from his own researches and those of Dr. Mitchell, that the evidence as to any evil thus caused is conflicting, but on the whole points to the evil being very small.

*Birds.*—In the case of the *Fowl* a whole array of authorities could be given against too close interbreeding. Sir J. Sebright positively asserts that he made many trials, and that his fowls, when thus treated, became long in the legs, small in the body, and bad breeders.<sup>31</sup> He produced the famous Sebright Bantams by complicated crosses, and by breeding in-and-in; and since his time there has been much close interbreeding with these animals; and they are now notoriously bad breeders. I have seen Silver Bantams, directly descended from his stock, which had become almost as barren as hybrids; for not a single chicken had been that year

<sup>29</sup> 'Descent of Man, 2nd. edit p. 524.

<sup>30</sup> 'Journal of Statistical Soc.' June, 1875, p. 153; and 'Fortnightly

Review,' June, 1875.

<sup>31</sup> 'The Art of Improving the Breed,' p. 13.

hatched from two full nests of eggs. Mr. Hewitt says that with these Bantams the sterility of the male stands, with rare exceptions, in the closest relation with their loss of certain secondary male characters: he adds, "I have noticed, as a general rule, that even the slightest deviation from feminine character in the tail of the male Sebright—say the elongation by only half an inch of the two principal tail feathers—brings with it improved probability of increased fertility."<sup>32</sup>

Mr. Wright states<sup>33</sup> that Mr. Clark, "whose fighting-cocks were so notorious, continued to breed from his own kind till they lost their disposition to fight, but stood to be cut up without making any resistance, and were so reduced in size as to be under those weights required for the best prizes; but on obtaining a cross from Mr. Leighton, they again resumed their former courage and weight." It should be borne in mind that game-cocks before they fought were always weighed, so that nothing was left to the imagination about any reduction or increase of weight. Mr. Clark does not seem to have bred from brothers and sisters, which is the most injurious kind of union; and he found, after repeated trials, that there was a greater reduction in weight in the young from a father paired with his daughter, than from a mother with her son. I may add that Mr. Eyton, of Eyton, the well-known ornithologist, who is a large breeder of Grey Dorkings, informs me that they certainly diminish in size, and become less prolific, unless a cross with another strain is occasionally obtained. So it is with Malays, according to Mr. Hewitt, as far as size is concerned.<sup>34</sup>

An experienced writer<sup>35</sup> remarks that the same amateur, as is well known, seldom long maintains the superiority of his birds; and this, he adds, undoubtedly is due to all his stock "being of the same blood;" hence it is indispensable that he should occasionally procure a bird of another strain. But this is not necessary with those who keep a stock of fowls at different stations. Thus, Mr. Ballance, who has bred Malays for thirty years, and has won more prizes with these birds than any other fancier in England, says that breeding in-and-in does not necessarily cause deterioration; "but all depends upon how this is managed." "My plan has been to keep about five or six distinct runs, and to rear about two hundred or three hundred chickens each year, and select the best birds from each run for crossing. I thus secure sufficient crossing to prevent deterioration."<sup>36</sup>

<sup>32</sup> 'The Poultry Book,' by W. B. Tegetmeier, 1866, p. 245.

<sup>33</sup> 'Journal Royal Agricult. Soc.,' 1846, vol. vii. p. 205; see also Ferguson on the Fowl, pp. 83, 317; see also 'The Poultry Book,' by Tegetmeier, 1866, p. 135, with respect to the extent to which cock-fighters found that they could venture to breed in-

and-in, viz., occasionally a hen with her own son; "but they were cautious not to repeat the in-and-in breeding."

<sup>34</sup> 'The Poultry Book,' by W. B. Tegetmeier, 1866, p. 79.

<sup>35</sup> 'The Poultry Chronicle,' 1854, vol. i. p. 43.

<sup>36</sup> 'The Poultry Book,' by W. B. Tegetmeier, 1866, p. 79.

We thus see that there is almost complete unanimity with poultry-breeders that, when fowls are kept at the same place, evil quickly follows from interbreeding carried on to an extent which would be disregarded in the case of most quadrupeds. Moreover, it is a generally received opinion that cross-bred chickens are the hardiest and most easily reared.<sup>37</sup> Mr. Tegetmeier, who has carefully attended to poultry of all breeds, says<sup>38</sup> that Dorking hens, allowed to run with Houdan or Crevecœur cocks, "produce in the early spring chickens that for size, hardihood, "early maturity, and fitness for the market, surpass those of any "pure breed that we have ever raised." Mr. Hewitt gives it as a general rule with fowls, that crossing the breed increases their size. He makes this remark after stating that hybrids from the pheasant and fowl are considerably larger than either progenitor: so again, hybrids from the male golden pheasant and female common pheasant "are of far larger size than either parent-bird."<sup>39</sup> To this subject of the increased size of hybrids I shall presently return.

With *Pigeons*, breeders are unanimous, as previously stated, that it is absolutely indispensable, notwithstanding the trouble and expense thus caused, occasionally to cross their much-prized birds with individuals of another strain, but belonging, of course, to the same variety. It deserves notice that, when size is one of the desired characters, as with pouters,<sup>40</sup> the evil effects of close interbreeding are much sooner perceived than when small birds, such as short-faced tumblers, are valued. The extreme delicacy of the high fancy breeds, such as these tumblers and improved English carriers, is remarkable; they are liable to many diseases, and often die in the egg or during the first moult; and their eggs have generally to be hatched under foster-mothers. Although these highly-prized birds have invariably been subjected to much close interbreeding, yet their extreme delicacy of constitution cannot perhaps be thus fully explained. Mr. Yarrell informed me that Sir J. Sebright continued closely interbreeding some owl-pigeons, until from their extreme sterility he as nearly as possible lost the whole family. Mr. Brent<sup>41</sup> tried to raise a breed of trumpeters, by crossing a common pigeon, and recrossing the daughter, granddaughter, great-granddaughter, and great-great-granddaughter, with the same male trumpeter, until he obtained a bird with  $\frac{1}{16}$  of trumpeter's blood; but then the experiment failed, for "breeding so close stopped reproduction." The experienced Neumeister<sup>42</sup> also asserts that the offspring from doves and various other breeds are "generally very fertile and

<sup>37</sup> 'The Poultry Chronicle,' vol. i. p. 89.

<sup>38</sup> 'The Poultry Book,' 1866, p. 210.

<sup>39</sup> *Ibid.* 1866, p. 167; and 'Poultry Chronicle,' vol. iii., 1855, p. 15.

<sup>40</sup> 'A Treatise on Fancy Pigeons,' by J. M. Eaton, p. 56.

<sup>41</sup> 'The Pigeon Book,' p. 46.

<sup>42</sup> 'Das Ganze der Taubenzucht,' 1837, s. 18.

hardy birds:" so again, MM. Boitard and Corbié,<sup>43</sup> after forty-five years' experience, recommend persons to cross their breeds for amusement; for, if they fail to make interesting birds, they will succeed under an economical point of view, "as it is found that mongrels are more fertile than pigeons of pure race."

I will refer only to one other animal, namely, the Hive-bee, because a distinguished entomologist has advanced this as a case of inevitable close interbreeding. As the hive is tenanted by a single female, it might have been thought that her male and female offspring would always have bred together, more especially as bees of different hives are hostile to each other; a strange worker being almost always attacked when trying to enter another hive. But Mr. Tegetmeier has shown<sup>44</sup> that this instinct does not apply to drones, which are permitted to enter any hive; so that there is no *à priori* improbability of a queen receiving a foreign drone. The fact of the union invariably and necessarily taking place on the wing, during the queen's nuptial flight, seems to be a special provision against continued interbreeding. However this may be, experience has shown, since the introduction of the yellow-banded Ligurian race into Germany and England, that bees freely cross: Mr. Woodbury, who introduced Ligurian bees into Devonshire, found during a single season that three stocks, at distances of from one to two miles from his hives, were crossed by his drones. In one case the Ligurian drones must have flown over the city of Exeter, and over several intermediate hives. On another occasion several common black queens were crossed by Ligurian drones at a distance of from one to three and a half miles.<sup>45</sup>

### *Plants.*

When a single plant of a new species is introduced into any country, if propagated by seed, many individuals will soon be raised, so that if the proper insects be present there will be crossing. With newly-introduced trees or other plants not propagated by seed we are not here concerned. With old-established plants it is an almost universal practice occasionally to make exchanges of seed, by which means individuals which have been exposed to different conditions of life,—and this, as we have seen with animals, diminishes the evil from close interbreeding,—will occasionally be introduced into each district.

With respect to individuals belonging to the same sub-variety, Gärtner, whose accuracy and experience exceeded that of all other observers, states<sup>46</sup> that he has many times observed good effects from this step, especially with exotic genera, of which the fertility is somewhat impaired, such as *Passiflora*, *Lobelia*, *Fuchsia*.

<sup>43</sup> 'Les Pigeons,' 1824, p. 35.

<sup>44</sup> 'Proc. Entomolog. Soc.,' Aug. 6th, 1860, p. 126.

<sup>46</sup> 'Journal of Horticulture,' 1861,

pp. 39, 77, 158; and 1864, p. 206.

<sup>46</sup> 'Beiträge zur Kenntniss der Befruchtung,' 1844, s. 366.



Herbert also says,<sup>47</sup> "I am inclined to think that I have derived "advantage from impregnating the flower from which I wished "to obtain seed with pollen from another individual of the same "variety, or at least from another flower, rather than with its "own." Again, Professor Lecoq ascertained that crossed offspring are more vigorous and robust than their parents.<sup>48</sup>

General statements of this kind, however, can seldom be fully trusted: I therefore began a long series of experiments, continued for about ten years, which will I think conclusively show the good effects of crossing two distinct plants of the same variety, and the evil effects of long-continued self-fertilisation. A clear light will thus be thrown on such questions, as why flowers are almost invariably constructed so as to permit, or favour, or necessitate the union of two individuals. We shall clearly understand why monœcious and dicecious,—why dichogamous, dimorphic and trimorphic plants exist, and many other such cases. I intend soon to publish an account of these experiments, and I can here give only a few cases in illustration. The plan which I followed was to grow plants in the same pot, or in pots of the same size, or close together in the open ground; carefully to exclude insects; and then to fertilise some of the flowers with pollen from the same flower, and others on the same plant with pollen from a distinct but adjoining plant. In many of these experiments, the crossed plants yielded much more seed than the self-fertilised plants; and I have never seen the reversed case. The self-fertilised and crossed seeds thus obtained were allowed to germinate in the same glass vessel on damp sand; and as the seeds germinated, they were planted in pairs on opposite sides of the same pot, with a superficial partition between them, and were placed so as to be equally exposed to the light. In other cases the self-fertilised and crossed seeds were simply sown on opposite sides of the same small pot. I have, in short, followed different plans, but in every case have taken all the precautions which I could think of, so that the two lots should be equally favoured. The growth of the plants raised from the crossed and self-fertilised seed, were carefully observed from their germination to maturity, in species belonging to fifty-two genera; and the difference in their growth, and in withstanding unfavourable conditions, was in most cases manifest and strongly marked. It is of importance that the two lots of seed should be sown or planted on opposite sides of the same pot, so that the seedlings may struggle against each other; for if sown separately in ample and good soil, there is often but little difference in their growth.

I will briefly describe two of the first cases observed by me. Six crossed and six self-fertilised seeds of *Ipomœa purpurea*, from plants treated in the manner above described, were planted as soon as they had germinated, in pairs on opposite sides of two pots, and rods of equal thickness were given them to twine up. Five

<sup>47</sup> 'Amaryllidacæ,' p. 371.

<sup>48</sup> 'De la Fécondation,' 2nd edit., 1862, p. 79.

of the crossed plants grew from the first more quickly than the opposed self-fertilised plants; the sixth, however, was weakly and was for a time beaten, but at last its sounder constitution prevailed and it shot ahead of its antagonist. As soon as each crossed plant reached the top of its seven-foot rod its fellow was measured, and the result was that, when the crossed plants were seven feet high the self-fertilised had attained the average height of only five feet four and a half inches. The crossed plants flowered a little before, and more profusely than the self-fertilised plants. On opposite sides of another *small* pot a large number of crossed and self-fertilised seeds were sown, so that they had to struggle for bare existence; a single rod was given to each lot: here again the crossed plants showed from the first their advantage; they never quite reached the summit of the seven-foot rod, but relatively to the self-fertilised plants their average height was as seven feet to five feet two inches. The experiment was repeated during several succeeding generations, treated in exactly the same manner, and with nearly the same result. In the second generation, the crossed plants, which were again crossed, produced 121 seed-capsules, whilst the self-fertilised, again self-fertilised, produced only 84 capsules.

Some flowers of the *Mimulus luteus* were fertilised with their own pollen, and others were crossed with pollen from distinct plants growing in the same pot. The seeds were thickly sown on opposite sides of a pot. The seedlings were at first equal in height; but when the young crossed plants were half an inch, the self-fertilised plants were only a quarter of an inch high. But this degree of inequality did not last, for, when the crossed plants were four and a half inches high, the self-fertilised were three inches, and they retained the same relative difference till their growth was complete. The crossed plants looked far more vigorous than the uncrossed, and flowered before them; they produced also a far greater number of capsules. As in the former case, the experiment was repeated during several succeeding generations. Had I not watched these plants of *Mimulus* and *Ipomoea* during their whole growth, I could not have believed it possible, that a difference apparently so slight as that of the pollen being taken from the same flower, or from a distinct plant growing in the same pot, could have made so wonderful a difference in the growth and vigour of the plants thus produced. This, under a physiological point of view, is a most remarkable phenomenon.

With respect to the benefit derived from crossing distinct varieties, plenty of evidence has been published. Sageret<sup>49</sup> repeatedly speaks in strong terms of the vigour of melons raised by crossing different varieties, and adds that they are more easily fertilised than common melons, and produce numerous good seed.

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<sup>49</sup> 'Mémoire sur les Cucurbitacées,' pp. 36, 28, 30.

Here follows the evidence of an English gardener:<sup>50</sup> "I have this summer met with better success in my cultivation of melons, in an unprotected state, from the seeds of hybrids (*i.e.* mongrels) obtained by cross impregnation, than with old varieties. The offspring of three different hybridisations (one more especially, of which the parents were the two most dissimilar varieties I could select) each yielded more ample and finer produce than any one of between twenty and thirty established varieties."

Andrew Knight<sup>51</sup> believed that his seedlings from crossed varieties of the apple exhibited increased vigour and luxuriance; and M. Chevreul<sup>52</sup> alludes to the extreme vigour of some of the crossed fruit-trees raised by Sageret.

By crossing reciprocally the tallest and shortest peas, Knight<sup>53</sup> says: "I had in this experiment a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet; whilst the height of the large and luxuriant kind was very little diminished." Mr. Laxton gave me seed-peas produced from crosses between four distinct kinds; and the plants thus raised were extraordinarily vigorous, being in each case from one to two or three feet taller than the parent-forms growing close alongside them.

Wiegmann<sup>54</sup> made many crosses between several varieties of cabbage; and he speaks with astonishment of the vigour and height of the mongrels, which excited the amazement of all the gardeners who beheld them. Mr. Chaundy raised a great number of mongrels by planting together six distinct varieties of cabbage. These mongrels displayed an infinite diversity of character; "But the most remarkable circumstance was, that, while all the other cabbages and borecoles in the nursery were destroyed by a severe winter, these hybrids were little injured, and supplied the kitchen when there was no other cabbage to be had."

Mr. Maund exhibited before the Royal Agricultural Society<sup>55</sup> specimens of crossed wheat, together with their parent varieties; and the editor states that they were intermediate in character, "united with that greater vigour of growth, which it appears, in the vegetable as in the animal world, is the result of a first cross." Knight also crossed several varieties of wheat,<sup>56</sup> and he says "that in the years 1795 and 1796, when almost the whole crop of corn in the island was blighted, the varieties thus obtained, and these only, escaped in this neighbourhood, though sown in several different soils and situations."

<sup>50</sup> Loudon's 'Gard. Mag.,' vol. viii., 1832, p. 52.

<sup>51</sup> 'Transact. Hort. Soc.,' vol. i. p. 5.

<sup>52</sup> 'Annal. des Sc. Nat.,' 3rd series, Bot., tom. vi. p. 189.

<sup>53</sup> 'Philosophical Transactions,' 1799, p. 200.

<sup>54</sup> 'Ueber die Bastardzeugung,' 1828, s. 32, 33. For Mr. Chaundy's case, see Loudon's 'Gard. Mag.' vol. vii. 1831, p. 696.

<sup>55</sup> 'Gardener's Chron.,' 1846, p. 601.

<sup>56</sup> 'Philosoph. Transact.,' 1799, p. 201.

Here is a remarkable case: M. Clotzsch<sup>57</sup> crossed *Pinus sylvestris* and *nigricans*, *Quercus robur* and *pedunculata*, *Alnus glutinosa* and *incana*, *Ulmus campestris* and *effusa*; and the cross-fertilised seeds, as well as seeds of the pure parent-trees, were all sown at the same time and in the same place. The result was, that after an interval of eight years, the hybrids were one-third taller than the pure trees!

The facts above given refer to undoubted varieties, excepting the trees crossed by Clotzsch, which are ranked by various botanists as strongly-marked races, sub-species, or species. That true hybrids raised from entirely distinct species, though they lose in fertility, often gain in size and constitutional vigour, is certain. It would be superfluous to quote any facts; for all experimenters, Kölreuter, Gärtner, Herbert, Sageret, Lecoq, and Naudin, have been struck with the wonderful vigour, height, size, tenacity of life, precocity, and hardness of their hybrid productions. Gärtner<sup>58</sup> sums up his conviction on this head in the strongest terms. Kölreuter<sup>59</sup> gives numerous precise measurements of the weight and height of his hybrids in his comparison with measurements of both parent-forms; and speaks with astonishment of their *statura portentosa*, their "*ambitus vastissimus ac altitudo valde conspicua*." Some exceptions to the rule in the case of very sterile hybrids have, however, been noticed by Gärtner and Herbert; but the most striking exceptions are given by Max Wichura,<sup>60</sup> who found that hybrid willows were generally tender in constitution, dwarf, and short-lived.

Kölreuter explains the vast increase in the size of the roots, stems, &c., of his hybrids, as the result of a sort of compensation due to their sterility, in the same way as many emasculated animals are larger than the perfect males. This view seems at first sight extremely probable, and has been accepted by various authors;<sup>61</sup> but Gärtner<sup>62</sup> has well remarked that there is much difficulty in fully admitting it; for with many hybrids there is no parallelism between the degree of their sterility and their increased size and vigour. The most striking instances of luxuriant growth have been observed with hybrids which were not sterile in any extreme degree. In the genus *Mirabilis*, certain hybrids are unusually fertile, and their extraordinary luxuriance of growth, together with

<sup>57</sup> Quoted in 'Bull. Bot. Soc. France,' vol. ii., 1855, p. 327.

<sup>58</sup> Gärtner, 'Bastarderzeugung,' s. 259, 518, 526 *et seq.*

<sup>59</sup> 'Fortsetzung,' 1763, s. 29; 'Dritte Fortsetzung,' s. 44, 96; 'Act. Acad. St. Petersburg,' 1782, part ii., p. 251; 'Nova Acta,' 1793, pp. 391, 394; 'Nova Acta,' 1795, pp. 316, 323.

<sup>60</sup> 'Die Bastardbefruchtung,' &c., 1865, s. 31, 41, 42.

<sup>61</sup> Max Wichura fully accepts this view ('Bastardbefruchtung,' s. 43), as does the Rev. M. J. Berkeley, in 'Journal of Hort. Soc.,' Jan. 1866, p. 70.

<sup>62</sup> 'Bastarderzeugung,' s. 394, 526, 528.

their enormous roots,<sup>63</sup> have been transmitted to their progeny. The result in all cases is probably in part due to the saving of nutriment and vital force through the sexual organs acting imperfectly or not at all, but more especially to the general law of good being derived from a cross. For it deserves especial attention that mongrel animals and plants, which are so far from being sterile that their fertility is often actually augmented, have, as previously shown, their size, hardiness, and constitutional vigour generally increased. It is not a little remarkable that an accession of vigour and size should thus arise under the opposite contingencies of increased and diminished fertility.

It is a perfectly well ascertained fact<sup>64</sup> that hybrids invariably breed with either pure parent, and not rarely with a distinct species, more readily than with one another. Herbert is inclined to explain even this fact by the advantage derived from a cross; but Gärtner more justly accounts for it by the pollen of the hybrid, and probably its ovules, being in some degree vitiated, whereas the pollen and ovules of both pure parents and of any third species are sound. Nevertheless, there are some well-ascertained and remarkable facts, which, as we shall presently see, show that a cross by itself undoubtedly tends to increase or re-establish the fertility of hybrids.

The same law, namely, that the crossed offspring both of varieties and species are larger than the parent-forms, holds good in the most striking manner with hybrid animals as well as with mongrels. Mr. Bartlett, who has had such large experience says, "Among all " hybrids of vertebrated animals there is a marked increase of size." He then enumerates many cases with mammals, including monkeys, and with various families of birds.<sup>65</sup>

*On certain Hermaphrodite Plants which, either normally or abnormally, require to be fertilised by pollen from a distinct individual or species.*

The facts now to be given differ from the foregoing, as self-sterility is not here the result of long-continued close interbreeding. These facts are, however, connected with our present subject, because a cross with a distinct individual is shown to be either necessary or advantageous. Dimorphic and trimorphic plants, though they are hermaphrodites, must be reciprocally crossed, one set of forms by the other, in order to be fully fertile, and in some cases to be fertile in any degree.

<sup>63</sup> Kölreuter, 'Nova Acta,' 1795, 430.  
p. 316.

<sup>65</sup> Quoted by Dr. Murie, in 'Proc. Zoolog. Soc.,' 1870, p. 40.

<sup>64</sup> Gärtner, 'Bastarderzeugung,' s.

But I should not have noticed these plants, had it not been for the following cases given by Dr. Hildebrand :<sup>66</sup>—

*Primula sinensis* is a reciprocally dimorphic species: Dr. Hildebrand fertilised twenty-eight flowers of both forms, each by pollen of the other form, and obtained the full number of capsules containing on an average 42·7 seed per capsule; here we have complete and normal fertility. He then fertilised forty-two flowers of both forms with pollen of the same form, but taken from a distinct plant, and all produced capsules containing on an average only 19·6 seed. Lastly, and here we come to our more immediate point, he fertilised forty-eight flowers of both forms with pollen of the same form and taken from the same flower, and now he obtained only thirty-two capsules, and these contained on an average 18·6 seed, or one less per capsule than in the former case. So that, with these illegitimate unions, the act of impregnation is less assured, and the fertility slightly less, when the pollen and ovules belong to the same flower, than when belonging to two distinct individuals of the same form. Dr. Hildebrand has recently made analogous experiments on the long-styled form of *Oxalis rosea*, with the same result.<sup>67</sup>

It has recently been discovered that certain plants, whilst growing in their native country under natural conditions, cannot be fertilised with pollen from the same plant. They are sometimes so utterly self-impotent, that, though they can readily be fertilised by the pollen of a distinct species or even distinct genus, yet, wonderful as is the fact, they never produce a single seed by their own pollen. In some cases, moreover, the plant's own pollen and stigma mutually act on each other in a deleterious manner. Most of the facts to be given relate to orchids, but I will commence with a plant belonging to a widely different family.

Sixty-three flowers of *Corydalis cava*, borne on distinct plants, were fertilised by Dr. Hildebrand<sup>68</sup> with pollen from other plants of the same species; and fifty-eight capsules were obtained, including on an average 4·5 seed in each. He then fertilised sixteen flowers produced by the same raceme, one with another, but obtained only three capsules, one of which alone contained any good seeds, namely, two in number. Lastly, he fertilised twenty-seven flowers, each with its own pollen; he left also fifty-seven flowers to be spontaneously fertilised, and this would certainly have ensued if it

<sup>66</sup> 'Botanische Zeitung,' Jan. 1864, Berlin, 1866, s. 372.  
s. 3.

<sup>68</sup> International Hort. Congress,

<sup>67</sup> 'Monatsbericht Akad. Wissen.' London, 1866.

had been possible, for the anthers not only touch the stigma, but the pollen-tubes were seen by Dr. Hildebrand to penetrate it; nevertheless these eighty-four flowers did not produce a single seed-capsule! This whole case is highly instructive, as it shows how widely different the action of the same pollen is, according as it is placed on the stigma of the same flower, or on that of another flower on the same raceme, or on that of a distinct plant.

With exotic Orchids several analogous cases have been observed, chiefly by Mr. John Scott.<sup>69</sup> *Oncidium sphacelatum* has effective pollen, for Mr. Scott fertilised two distinct species with it; the ovules are likewise capable of impregnation, for they were readily fertilised by the pollen of *O. divaricatum*; nevertheless, between one and two hundred flowers fertilised by their own pollen did not produce a single capsule, though the stigmas were penetrated by the pollen-tubes. Mr. Robertson Munro, of the Royal Botanic Gardens of Edinburgh, also informs me (1864) that a hundred and twenty flowers of this same species were fertilised by him with their own pollen, and did not produce a capsule, but eight flowers, fertilised by the pollen of *O. divaricatum*, produced four fine capsules: again, between two and three hundred flowers of *O. divaricatum*, fertilised by their own pollen, did not set a capsule, but twelve flowers fertilised by *O. flexuosum* produced eight fine capsules: so that here we have three utterly self-impotent species, with their male and female organs perfect, as shown by their mutual fertilisation. In these cases fertilisation was effected only by the aid of a distinct species. But, as we shall presently see, distinct plants, raised from seed, of *Oncidium flexuosum*, and probably of the other species, would have been perfectly capable of fertilising each other, for this is the natural process. Again, Mr. Scott found that the pollen of a plant of *O. microchilum* was effective, for with it he fertilised two distinct species; he found its ovules good, for they could be fertilised by the pollen of one of these species, and by the pollen of a distinct plant of *O. microchilum*; but they could not be fertilised by pollen of the same plant, though the pollen-tubes penetrated the stigma. An analogous case has been recorded by M. Rivière,<sup>70</sup> with two plants of *O. cavendishianum*, which were both self-sterile, but reciprocally fertilised each other. All these cases refer to the genus *Oncidium*, but Mr. Scott found that *Maxillaria atro-rubens* was "totally insusceptible of fertilisation with its own pollen," but fertilised, and was fertilised by, a widely distinct species, viz. *M. squalens*.

As these orchids had been grown under unnatural conditions in hot-houses, I concluded that their self-sterility was due to this cause. But Fritz Müller informs me that at Desterro, in Brazil, he

<sup>69</sup> 'Proc. Bot. Soc. of Edinburgh,' May, 1863: these observations are given in abstract, and others are added, in the 'Journal of Proc. of

Linn. Soc.,' vol. viii. Bot., 1864, p. 162.

<sup>70</sup> Prof. Lecoq, 'De la Fécondation,' 2nd edit., 1862, p. 76.

fertilised above one hundred flowers of the above-mentioned *Oncidium flexuosum*, which is there endemic, with its own pollen, and with that taken from distinct plants: all the former were sterile, whilst those fertilised by pollen from any *other plant* of the same species were fertile. During the first three days there was no difference in the action of the two kinds of pollen: that placed on stigma of the same plant separated in the usual manner into grains, and emitted tubes which penetrated the column, and the stigmatic chamber shut itself; but only those flowers which had been fertilised by pollen taken from a distinct plant produced seed-capsules. On a subsequent occasion these experiments were repeated on a large scale with the same result. Fritz Müller found that four other endemic species of *Oncidium* were in like manner utterly sterile with their own pollen, but fertile with that from any other plant: some of them likewise produced seed-capsules when impregnated with pollen of widely distinct genera, such as *Cyrtopodium*, and *Rodriguezia*. *Oncidium crispum*, however, differs from the foregoing species in varying much in its self-sterility; some plants producing fine pods with their own pollen, others failing to do so in two or three instances, Fritz Müller observed that the pods produced by pollen taken from a distinct flower on the same plant, were larger than those produced by the flower's own pollen. In *Epidendrum cinnabarinum*, an orchid belonging to another division of the family, fine pods were produced by the plant's own pollen, but they contained by weight only about half as much seed as the capsules which had been fertilised by pollen from a distinct plant, and in one instance from a distinct species; moreover, a very large proportion, and in some cases nearly all the seeds produced by the plant's own pollen, were destitute of an embryo. Some self-fertilised capsules of a *Maxillaria* were in a similar state.

Another observation made by Fritz Müller is highly remarkable, namely, that with various orchids the plant's own pollen not only fails to impregnate the flower, but acts on the stigma, and is acted on, in an injurious or poisonous manner. This is shown by the surface of the stigma in contact with the pollen, and by the pollen itself, becoming in from three to five days dark brown, and then decaying. The discoloration and decay are not caused by parasitic cryptogams, which were observed by Fritz Müller in only a single instance. These changes are well shown by placing on the same stigma, at the same time, the plant's own pollen and that from a distinct plant of the same species, or of another species, or even of another and widely remote genus. Thus, on the stigma of *Oncidium flexuosum*, the plant's own pollen and that from a distinct plant were placed side by side, and in five days' time the latter was perfectly fresh, whilst the plant's own pollen was brown. On the other hand, when the pollen of a distinct plant of the *Oncidium flexuosum* and of the *Epidendrum zebra* (*nov. spec.?*) were placed together on the same stigma, they behaved in exactly the same manner, the grains separating, emitting tubes,



and penetrating the stigma, so that the two pollen-masses, after an interval of eleven days, could not be distinguished except by the difference of their caudicles, which, of course, undergo no change. Fritz Müller has, moreover, made a large number of crosses between orchids belonging to distinct species and genera, and he finds that in all cases when the flowers are not fertilised their footstalks first begin to wither; and the withering slowly spreads upwards until the germen fall off, after an interval of one or two weeks, and in one instance of between six and seven weeks; but even in this latter case, and in most other cases, the pollen and stigma remained in appearance fresh. Occasionally, however, the pollen becomes brownish, generally on the external surface, and not in contact with the stigma, as is invariably the case when the plant's own pollen is applied.

Fritz Müller observed the poisonous action of the plant's own pollen in the above-mentioned *Oncidium flexuosum*, *O. unicorn*, *pubes* (?), and in two other unnamed species. Also in two species of *Rodriguezia*, in two of *Notylia*, in one of *Burlingtonia*, and of a fourth genus in the same group. In all these cases, except the last, it was proved that the flowers were, as might have been expected, fertile with pollen from a distinct plant of the same species. Numerous flowers of one species of *Notylia* were fertilised with pollen from the same raceme; in two days' time they all withered, the germen began to shrink, the pollen-masses became dark brown, and not one pollen-grain emitted a tube. So that in this orchid the injurious action of the plant's own pollen is more rapid than with *Oncidium flexuosum*. Eight other flowers on the same raceme were fertilised with pollen from a distinct plant of the same species: two of these were dissected, and their stigmas were found to be penetrated by numberless pollen-tubes; and the germen of the other six flowers became well developed. On a subsequent occasion many other flowers were fertilised with their own pollen, and all fell off dead in a few days; whilst some flowers on the same raceme which had been left simply unfertilised adhered and long remained fresh. We have seen that in cross-unions between extremely distinct orchids the pollen long remains undecayed; but *Notylia* behaved in this respect differently; for when its pollen was placed on the stigma of *Oncidium flexuosum*, both the stigma and pollen quickly became dark brown, in the same manner as if the plant's own pollen had been applied.

Fritz Müller suggests that, as in all these cases the plant's own pollen is not only impotent (thus effectually preventing self-fertilisation), but likewise prevents, as was ascertained in the case of the *Notylia* and *Oncidium flexuosum*, the action of subsequently applied pollen from a distinct individual, it would be an advantage to the plant to have its own pollen rendered more and more deleterious; for the germen would thus quickly be killed, and dropping off, there would be no further waste in nourishing a part which ultimately could be of no avail

The same naturalist found in Brazil three plants of a *Bignonia* growing near together. He fertilised twenty-nine flowerets on one of them with their own pollen, and they did not set a single capsule. Thirty flowers were then fertilised with pollen from a distinct plant, one of the three, and they yielded only two capsules. Lastly, five flowers were fertilised with pollen from a fourth plant growing at a distance, and all five produced capsules. Fritz Müller thinks that the three plants which grew near one another were probably seedlings from the same parent, and that from being closely related, they acted very feebly on one another. This view is extremely probable, for he has since shown in a remarkable paper,<sup>71</sup> that in the case of some Brazilian species of *Abutilon*, which are self-sterile, and between which he raised some complex hybrids, that these, if near relatives, were much less fertile *inter se*, than when not closely related.

We now come to cases closely analogous with those just given, but different in so far that only certain individuals of the species are self-sterile. This self-impotence does not depend on the pollen or ovules being in an unfit state for fertilisation, for both have been found effective in union with other plants of the same or of a distinct species. The fact of plants having acquired so peculiar a constitution, that they can be fertilised more readily by the pollen of a distinct species than by their own, is exactly the reverse of what occurs with all ordinary species. For in the latter the two sexual elements of the same individual plant are of course capable of freely acting on each other; but are so constituted that they are more or less impotent when brought into union with the sexual elements of a distinct species, and produce more or less sterile hybrids.

Gärtner experimented on two plants of *Lobelia fulgens*, brought from separate places, and found<sup>72</sup> that their pollen was good, for he fertilised with it *L. cardinalis* and *siphilitica*; their ovules were likewise good, for they were fertilised by the pollen of these same two species; but these two plants of *L. fulgens* could not be fertilised by their own pollen, as can generally be effected with perfect ease with this species. Again, the pollen of a plant of *Verbascum nigrum* grown in a pot was found by Gärtner<sup>73</sup> capable of fertilising *V. lychnitis* and *V. austriacum*; the ovules could be fertilised by the

<sup>71</sup> 'Jenaische Zeitschrift für Naturwiss.' B. vii. p. 22, 1872, and p. 441, 1873. A large part of this paper has been translated in the 'American

Naturalist,' 1874, p. 223.

<sup>72</sup> 'Bastarderzeugung,' s. 64, 357.

<sup>73</sup> Ibid., s. 357.

pollen of *V. thapsus*; but the flowers could not be fertilised by their own pollen. Kölreuter, also,<sup>74</sup> gives the case of three garden plants of *Verbascum phoeniceum*, which bore during two years many flowers; these he fertilised successfully with the pollen of no less than four distinct species, but they produced not a seed with their own apparently good pollen; subsequently these same plants, and others raised from seed, assumed a strangely fluctuating condition, being temporarily sterile on the male or female side, or on both sides, and sometimes fertile on both sides; but two of the plants were perfectly fertile throughout the summer.

With *Reseda odorata* I have found certain individuals quite sterile with their own pollen, and so it is with the indigenous *Reseda lutea*. The self-sterile plants of both species were perfectly fertile when crossed with pollen from any other individual of the same species. These observations will hereafter be published in another work, in which I shall also show that seeds sent to me by Fritz Müller produced by plants of *Eschscholtzia californica* which were quite self-sterile in Brazil, yielded in this country plants which were only slightly self-sterile.

It appears<sup>75</sup> that certain flowers on certain plants of *Lilium candidum* can be fertilised more freely by pollen from a distinct individual than by their own. So, again, with the varieties of the potato. Tinzmann,<sup>76</sup> who made many trials with this plant, says that pollen from another variety sometimes "exerts a powerful influence, and I have found sorts of potatoes which would not bear seed from impregnation with the pollen of their own flowers" would bear it when impregnated with other pollen." It does not, however, appear to have been proved that the pollen which failed to act on the flower's own stigma was in itself good.

In the genus *Passiflora* it has long been known that several species do not produce fruit, unless fertilised by pollen taken from distinct species: thus, Mr. Mowbray<sup>77</sup> found that he could not get fruit from *P. alata* and *racemosa* except by reciprocally fertilising them with each other's pollen; and similar facts have been observed in Germany and France.<sup>78</sup> I have received two accounts of *P. quadrangularis* never producing fruit from its own pollen, but doing so freely when fertilised in one case with the pollen of *P. cœrulea*, and in another case with that of *P. edulis*. But in three

<sup>74</sup> 'Zweite Fortsetzung,' s. 10; 'Dritte Forts.,' s. 40. Mr. Scott likewise fertilised fifty-four flowers of *Verbascum phoeniceum*, including two varieties, with their own pollen, and not a single capsule was produced. Many of the pollen-grains emitted their tubes, but only a few of them penetrated the stigmas; some slight effect however was produced, as many of the ovaries became somewhat

developed: 'Journal Asiatic Soc. Bengal,' 1867, p. 150.

<sup>75</sup> Duvernoy, quoted by Gärtner, 'Bastarderzeugung,' s. 334.

<sup>76</sup> 'Gardener's Chronicle,' 1846, p. 183.

<sup>77</sup> 'Transact. Hort. Soc.,' vol. vii., 1830, p. 95.

<sup>78</sup> Prof. Lecoq, 'De la Fécondation,' 1845, p. 70; Gärtner, 'Bastarderzeugung,' s. 64.

other cases this species fruited freely when fertilised with its own pollen; and the writer in one case attributed the favourable result to the temperature of the house having been raised from 5° to 10° Fahr. above the former temperature, after the flowers were fertilised.<sup>79</sup> With respect to *P. laurifolia*, a cultivator of much experience has recently remarked<sup>80</sup> that the flowers "must be fertilised with the pollen of *P. cœrulea*, or of some other common kind, as their own pollen will not fertilise them." But the fullest details on this subject have been given by Messrs. Scott and Robertson Munro:<sup>81</sup> plants of *P. assiflora racemosa*, *cœrulea*, and *alata* flowered profusely during many years in the Botanic Gardens of Edinburgh, and, though repeatedly fertilised with their own pollen, never produced any seed; yet this occurred at once with all three species when they were crossed together in various ways. In the case of *P. cœrulea* three plants, two of which grew in the Botanic Gardens, were all rendered fertile, merely by impregnating each with pollen of one of the others. The same result was attained in the same manner with *P. alata*, but with only one plant out of three. As so many self-sterile species of *Passiflora* have been mentioned, it should be stated that the flowers of the annual *P. gracilis* are nearly as fertile with their own pollen as with that from a distinct plant; thus sixteen flowers spontaneously self-fertilised produced fruit, each containing on an average 21·3 seed, whilst fruit from fourteen crossed flowers contained 24·1 seed.

Returning to *P. alata*, I have received (1866) some interesting details from Mr. Robertson Munro. Three plants, including one in England, have already been mentioned which were inveterately self-sterile, and Mr. Munro informs me of several others which, after repeated trials during many years, have been found in the same predicament. At some other places, however, this species fruits readily when fertilised with its own pollen. At Taymouth Castle there is a plant which was formerly grafted by Mr. Donaldson on a distinct species, name unknown, and ever since the operation it has produced fruit in abundance by its own pollen; so that this small and unnatural change in the state of this plant has restored its self-fertility! Some of the seedlings from the Taymouth Castle plant were found to be not only sterile with their own pollen, but with each other's pollen, and with the pollen of distinct species. Pollen from the Taymouth plant failed to fertilise certain plants of the same species, but was successful on one plant in the Edinburgh Botanic Gardens. Seedlings were raised from this latter union, and some of their flowers were fertilised by Mr. Munro with their own pollen; but they were found to be as self-impotent as the mother-plant had always proved, except when fertilised by the grafted

<sup>79</sup> 'Gard. Chron.,' 1868, p. 1341.

<sup>80</sup> 'Gardener's Chron.,' 1866, p. 1068.

<sup>81</sup> 'Journal of Proc. of Linn. Soc.,'

vol. viii., 1864, p. 1168. Mr. Robertson Munro, in 'Trans. Bot. Soc.' of Edinburgh, vol. ix. p. 399.

Taymouth plant, and except, as we shall see, when fertilised by her own seedlings. For Mr. Munro fertilised eighteen flowers on the self-impotent mother-plant with pollen from these her own self-impotent seedlings, and obtained, remarkable as the fact is, eighteen fine capsules full of excellent seed! I have met with no case in regard to plants which shows so well as this of *P. alata*, on what small and mysterious causes complete fertility or complete sterility depends.

The facts hitherto given relate to the much-lessened or completely destroyed fertility of pure species when impregnated with their own pollen, in comparison with their fertility when impregnated by distinct individuals or distinct species; but closely analogous facts have been observed with hybrids.

Herbert states<sup>82</sup> that having in flower at the same time nine hybrid *Hippeastrums*, of complicated origin, descended from several species, he found that "almost every flower touched with pollen from another cross produced seed abundantly, and those which were touched with their own pollen either failed entirely, or formed slowly a pod of inferior size, with fewer seeds." In the 'Horticultural Journal' he adds that "the admission of the pollen of another cross-bred *Hippeastrum* (however complicated the cross) to any one flower of the number, is almost sure to check the fructification of the others." In a letter written to me in 1839, Dr. Herbert says that he had already tried these experiments during five consecutive years, and he subsequently repeated them, with the same invariable result. He was thus led to make an analogous trial on a pure species, namely, on the *Hippeastrum aulicum*, which he had lately imported from Brazil: this bulb produced four flowers, three of which were fertilised by their own pollen, and the fourth by the pollen of a triple cross between *H. bulbosum*, *reginæ*, and *vittatum*; the result was, that "the ovaries of the three first flowers soon ceased to grow, and after a few days perished entirely: whereas the pod impregnated by the hybrid made vigorous and rapid progress to maturity, and bore good seed, which vegetated freely." This is, indeed, as Herbert remarks, "a strange truth," but not so strange as it then appeared.

As a confirmation of these statements, I may add that Mr. M. Mayes,<sup>83</sup> after much experience in crossing the species of *Amaryllis* (*Hippeastrum*), says, "neither the species nor the hybrids will, we are well aware, produce seed so abundantly from their own pollen as from that of others." So, again, Mr. Bidwell, in New

<sup>82</sup> 'Amaryllidaceæ,' 1837, p. 371; 'Journal of Hort. Soc.,' vol. ii., 1847, p. 19.

<sup>83</sup> Loudon's 'Gardener's Magazine,' vol. xi., 1835, p. 260.

South Wales,<sup>84</sup> asserts that *Amaryllis belladonna* bears many more seeds when fertilised by the pollen of *Brunswigia* (*Amaryllis* of some authors) *joséphineæ* or of *B. multiflora*, than when fertilised by its own pollen. Mr. Beaton dusted four flowers of a *Cyrtanthus* with their own pollen, and four with the pollen of *Vallota* (*Amaryllis*) *purpurea*; on the seventh day "those which received their own pollen slackened their growth, and ultimately perished; those " which were crossed with the *Vallota* held on."<sup>85</sup> These latter cases, however, relate to uncrossed species, like those before given with respect to *Passiflora*, *Orchids*, &c., and are here referred to only because the plants belong to the same group of *Amaryllidaceæ*.

In the experiments on the hybrid *Hippeastrums*, if Herbert had found that the pollen of two or three kinds alone had been more efficient on certain kinds than their own pollen, it might have been argued that these, from their mixed parentage, had a closer mutual affinity than the others; but this explanation is inadmissible, for the trials were made reciprocally backwards and forwards on nine different hybrids; and a cross, whichever way taken, always proved highly beneficial. I can add a striking and analogous case from experiments made by the Rev. A. Rawson, of Bromley Common, with some complex hybrids of *Gladiolus*. This skilful horticulturist possessed a number of French varieties, differing from each other only in the colour and size of the flowers, all descended from *Gandavensis*, a well-known old hybrid, said to be descended from *G. natalensis* by the pollen of *G. oppositiflorus*.<sup>86</sup> Mr. Rawson, after repeated trials, found that none of the varieties would set seed with their own pollen, although taken from distinct plants of the same variety (which had, of course, been propagated by bulbs), but that they all seeded freely with pollen from any other variety. To give two examples: *Ophir* did not produce a capsule with its own pollen, but when fertilised with that of *Janire*, *Brenchleyensis*, *Vulcain* and *Linné*, it produced ten fine capsules; but the pollen of *Ophir* was good, for when *Linné* was fertilised by it seven capsules were produced. This latter variety, on the other hand, was utterly barren with its own pollen, which we have seen was perfectly efficient on *Ophir*. Altogether, Mr. Rawson, in the year 1861, fertilised twenty-six flowers borne by four varieties with pollen taken from other varieties, and every single flower produced a fine seed-capsule; whereas fifty-two flowers on the same plants, fertilised at the same time with their own pollen, did not yield a single seed-capsule. Mr. Rawson fertilised, in some cases, the alternate flowers,

<sup>84</sup> 'Gardener's Chronicle,' 1850, p. 470.

<sup>85</sup> 'Journal Hort. Soc.,' vol. v. p. 135. The seedlings thus raised were given to the Hort. Soc.; but I find, on inquiry, that they unfortunately died the following winter.

<sup>86</sup> Mr. D. Beaton, in 'Journal of

Hort.,' 1861, p. 453. Lecoq, however ('De la Fécond.,' 1862, p. 369), states that this hybrid is descended from *G. psittacinus* and *cardinalis*; but this is opposed to Herbert's experience, who found that the former species could not be crossed.

and in other cases all those down one side of the spike, with pollen of other varieties, and the remaining flowers with their own pollen. I saw these plants when the capsules were nearly mature, and their curious arrangement at once brought full conviction to the mind that an immense advantage had been derived from crossing these hybrids.

Lastly, I have heard from Dr. E. Bornet, of Antibes, who has made numerous experiments in crossing the species of *Cistus*, but has not yet published the results, that, when any of these hybrids are fertile, they may be said to be, in regard to function, dioecious; "for the flowers are always sterile when the pistil is fertilised by pollen taken from the same flower or from flowers on the same plant. But they are often fertile if pollen be employed from a distinct individual of the same hybrid nature, or from a hybrid made by a reciprocal cross."

*Conclusion.*—That plants should be self-sterile, although both sexual elements are in a fit state for reproduction, appears at first sight opposed to all analogy. With respect to the species, all the individuals of which are in this state, although living under their natural conditions, we may conclude that their self-sterility has been acquired for the sake of effectually preventing self-fertilisation. The case is closely analogous with that of dimorphic and trimorphic or heterostyled plants, which can be fully fertilised only by plants belonging to a different form, and not, as in the foregoing cases, indifferently by any other individual of the species. Some of these heterostyled plants are completely sterile with pollen taken from the same plant or from the same form. With respect to species living under their natural conditions, of which only certain individuals are self-sterile (as with *Reseda lutea*), it is probable that these have been rendered self-sterile to ensure occasional cross-fertilisation, whilst other individuals have remained self-fertile to ensure the propagation of the species. The case seems to be parallel with that of plants which produce, as Hermann Müller has discovered, two forms—one bearing more conspicuous flowers with their structure adapted for cross-fertilisation by insects, and the other form with less conspicuous flowers adapted for self-fertilisation. The self-sterility, however, of some of the foregoing plants is incidental on the conditions to which they have been subjected, as with the *Eschscholtzia*, the *Verbascum phœ-*

*niceum* (the sterility of which varied according to the season), and with the *Passiflora alata*, which recovered its self-fertility when grafted on a different stock.

It is interesting to observe in the above several cases the graduated series from plants which, when fertilised by their own pollen, yield the full number of seeds, but with the seedlings a little dwarfed in stature—to plants which when self-fertilised yield few seeds—to those which yield none, but have their ovaria somewhat developed—and, lastly, to those in which the plant's own pollen and stigma mutually act on one another like poison. It is also interesting to observe on how slight a difference in the nature of the pollen or of the ovules complete self-sterility or complete self-fertility must depend in some of the above cases. Every individual of the self-sterile species appears to be capable of producing the full complement of seed when fertilised by the pollen of any other individual (though judging from the facts given with respect to *Abutilon* the nearest kin must be excepted); but not one individual can be fertilised by its own pollen. As every organism differs in some slight degree from every other individual of the same species, so no doubt it is with their pollen and ovules; and in the above cases we must believe that complete self-sterility and complete self-fertility depend on such slight differences in the ovules and pollen, and not their having been differentiated in some special manner in relation to one another; for it is impossible that the sexual elements of many thousand individuals should have been specialised in relation to every other individual. In some, however, of the above cases, as with certain *Passifloras*, an amount of differentiation between the pollen and ovules sufficient for fertilisation is gained only by employing pollen from a distinct species; but this is probably the result of such plants having been rendered somewhat sterile from the unnatural conditions to which they have been exposed.

Exotic animals confined in menageries are sometimes in nearly the same state as the above-described self-impotent plants; for, as we shall see in the following chapter, certain monkeys, the larger carnivora, several finches, geese, and pheasants, cross together, quite as freely as, or even more



freely than the individuals of the same species breed together. Cases will, also, be given of sexual incompatibility between certain male and female domesticated animals, which, nevertheless, are fertile when matched with any other individual of the same kind.

In the early part of this chapter it was shown that the crossing of individuals belonging to distinct families of the same race, or to different races or species, gives increased size and constitutional vigour to the offspring, and, except in the case of crossed species, increased fertility. The evidence rests on the universal testimony of breeders (for it should be observed that I am not here speaking of the evil results of close interbreeding), and is practically exemplified in the higher value of cross-bred animals for immediate consumption. The good results of crossing have also been demonstrated with some animals and with numerous plants, by actual weight and measurement. Although animals of pure blood will obviously be deteriorated by crossing, as far as their characteristic qualities are concerned, there seems to be no exception to the rule that advantages of the kind just mentioned are thus gained, even when there has not been any previous close interbreeding; and the rule applies to such animals as cattle and sheep, which can long resist breeding in-and-in between the nearest blood-relations.

In the case of crossed species, although size, vigour, precocity, and hardiness are, with rare exceptions, gained, fertility, in a greater or less degree, is lost; but the gain in the above respects can hardly be attributed to the principle of compensation; for there is no close parallelism between the increased size and vigour of hybrid offspring and their sterility. Moreover, it has been clearly proved that mongrels which are perfectly fertile gain these same advantages as well as sterile hybrids.

With the higher animals no special adaptations for ensuring occasional crosses between distinct families seem to exist. The eagerness of the males, leading to severe competition between them, is sufficient; for even with gregarious animals, the old and dominant males will be dispossessed after a time and it would be a mere chance if a closely related member

of the same family were to be the victorious successor. The structure of many of the lower animals, when they are hermaphrodites, is such as to prevent the ovules being fertilised by the male element of the same individual; so that the concourse of two individuals is necessary. In other cases the access of the male element of a distinct individual is at least possible. With plants, which are affixed to the ground and cannot wander from place to place like animals, the numerous adaptations for cross-fertilisation are wonderfully perfect, as has been admitted by every one who has studied the subject.

The evil consequences of long-continued close interbreeding are not so easily recognised as the good effects from crossing, for the deterioration is gradual. Nevertheless, it is the general opinion of those who have had most experience, especially with animals which propagate quickly, that evil does inevitably follow sooner or later, but at different rates with different animals. No doubt a false belief may, like a superstition, prevail widely; yet it is difficult to suppose that so many acute observers have all been deceived at the expense of much cost and trouble. A male animal may sometimes be paired with his daughter, granddaughter, and so on, even for seven generations, without any manifest bad result: but the experiment has never been tried of matching brothers and sisters, which is considered the closest form of interbreeding, for an equal number of generations. There is good reason to believe that by keeping the members of the same family in distinct bodies, especially if exposed to somewhat different conditions of life, and by occasionally crossing these families, the evil results of interbreeding may be much diminished or quite eliminated. These results are loss of constitutional vigour, size, and fertility; but there is no necessary deterioration in the general form of the body, or in other good qualities. We have seen that with pigs first-rate animals have been produced after long-continued close interbreeding, though they had become extremely infertile when paired with their near relations. The loss of fertility, when it occurs, seems never to be absolute, but only relative to animals of the same blood; so that this sterility is to a certain

extent analogous with that of self-impotent plants which cannot be fertilised by their own pollen, but are perfectly fertile with pollen of any other individual of the same species. The fact of infertility of this peculiar nature being one of the results of long-continued interbreeding, shows that interbreeding does not act merely by combining and augmenting various morbid tendencies common to both parents; for animals with such tendencies, if not at the time actually ill, can generally propagate their kind. Although offspring descended from the nearest blood-relations are not necessarily deteriorated in structure, yet some authors believe that they are eminently liable to malformations; and this is not improbable, as everything which lessens the vital powers acts in this manner. Instances of this kind have been recorded in the case of pigs, bloodhounds, and some other animals.

Finally, when we consider the various facts now given which plainly show that good follows from crossing, and less plainly that evil follows from close interbreeding, and when we bear in mind that with very many organisms elaborate provisions have been made for the occasional union of distinct individuals, the existence of a great law of nature is almost proved; namely, that the crossing of animals and plants which are not closely related to each other is highly beneficial or even necessary, and that interbreeding prolonged during many generations is injurious.