In this chapter Darwin tightens the link between varieties and species even further. At the time, many people believed in the independent, divine creation of separate species, and in the absolute reproductive isolation between those species. Here, however, Darwin shows that the members of some plant and animal species can be successfully mated with members of other species and still produce viable offspring, offspring that are themselves sometimes capable of reproducing. He also shows that although most varieties can be successfully crossed with other varieties of the same species, that is not always the case: some varieties, when mated with members of other varieties of the same species, produce no viable offspring. Indeed, there are intriguing gradations of infertility even within a variety, for plants that produce several forms of flower. This all provides strong support for Darwin’s argument that species and varieties are really just points on a continuum of change, and that varieties are species in the making. Species may eventually become reproductively isolated from the members of other species, but they were not created that way. Note that Darwin does not consider the role of behavioral or other “pre-zygotic” (i.e., pre-mating) isolating mechanisms in this chapter; “matings” were forced in all of the examples that he discusses. He is concerned only with whether or not species and varieties are physiologically capable of cross-mating and producing fertile offspring.

Many naturalists believe that all species have been specially endowed with sterility\(^1\) when crossed (i.e., mated) with individuals of a different species, in order to prevent their confusion. This view certainly seems likely, for different species living in the same place could hardly have been kept distinct if they
had been able to freely interbreed. The subject is an important one for us, particularly as the sterility of species when first crossed, and that of their hybrid offspring, cannot, as I shall soon show, have been acquired through the preservation of successive, advantageous degrees of sterility. Sterility must instead be an incidental result of some as-yet little understood differences in the reproductive systems of the parent species.

In treating this subject, two classes of fundamentally different facts have generally been confounded: a) the sterility of species when first cross-mated, and 2) the sterility of the hybrids that are produced from successful crosses between members of different species.

The members of all distinct species have, of course, perfectly functional organs of reproduction. Yet, when a member of one species is mated with a member of another species, the mating usually produces either few or no offspring. The reproductive organs of hybrids, on the other hand, are functionally impotent, even though the reproductive organs themselves are structurally perfect, as revealed by microscopic examination. Similarly, in the case of matings between the members of two distinct species, the two sexual elements (the sperm and the egg) that go to form the embryo are perfect; but in hybrids they are either not developed at all, or are developed imperfectly. These distinctions are important when considering the cause of the sterility that is common to the two cases: it clearly must be caused through different mechanisms. The distinction probably has been slurred over by other authors simply because the sterility in both cases has typically been considered a special divine endowment beyond the province of our reasoning powers.

The fact that varieties— that is, different forms that are known or at least believed to be descended from common parents—as well as their mongrel offspring, can be successfully crossed to obtain viable offspring is, according to my theory, also important in considering the sterility of species, as it seems to make a broad and very clear distinction between varieties and species. I discuss this point later in this chapter.
**Degrees of Sterility**

PREVIEW: Here Darwin shows that for plants, some crosses between the members of different species produce no offspring, as expected, while others are fully fertile, and also that some crosses result in seed production that is reduced to various degrees. That is, there is a continuum of sterility; sterility is not absolute. Moreover, he argues that although hybrids have been said to have decreased fertility, this is probably due to procedural errors in the experiments conducted: Darwin shows that in many cases both plant and animal hybrids are perfectly fertile for many generations. Thus, Darwin argues, there is no well-defined law that species cannot interbreed. Rather, degrees of sterility between the members of different species vary with circumstance.

First let us consider the sterility of species when crossed and of their hybrid offspring. I hope to convince you that neither sterility after matings between the members of different groups or fertility provides any convincing evidence of whether the two groups represent separate species or merely varieties of a single species. It is impossible to study the several memoirs and works of those two conscientious and admirable observers, the well-known German botanists Joseph Gottleib Kölreuter and Karl Friedrich von Gärtner, who devoted nearly their entire lives to this subject, without being deeply impressed with the high generality of at least some degree of sterility resulting from matings between members of different species. Kölreuter makes the rule of sterility universal for such matings, but then he cuts the Gordian Knot⁵, for in the 10 cases in which he found two forms that most authors have considered to be distinct species to be quite fertile when mated together, he unhesitatingly ranks them as mere varieties of the same species, and not as separate species after all!

Gärtner also makes the rule of sterility universal, and accordingly disputes all 10 of Kölreuter’s cases of unexpected fertility. But in these and in many other cases, Gärtner is obliged to carefully count
the seeds produced after the matings, in order to show that there is at least some degree of sterility; for Gärtnert, sterility simply means a decline in fertility, not a total failure of reproduction. He always compares the maximum number of seeds produced by two species when first crossed (and the maximum number produced by their hybrid offspring) with the average number produced by both pure parent-species in nature. He makes the same comparison between maximum seed production by the hybrid offspring and the average number produced from crosses between the pure parents. But a plant, to be reliably hybridized, must be castrated, and, even more importantly, must be isolated from other plants, in order to prevent pollen from being brought to it by insects that have visited flowers on other plants. Unfortunately, nearly all the plants experimented on by Gärtnert were potted, and kept in a chamber in his house. There is no doubt that such processes are often injurious to plant fertility. Indeed, Gärtnert gives in his table of data about 12 examples of plants that he castrated and then artificially fertilized with their own pollen (i.e., they were self-fertilized), and, excluding certain groups in which that manipulation is difficult to make, half of these 20 plants had their fertility impaired to at least some degree. Moreover, as Gärtnert crossed some forms repeatedly with their own pollen, such as the common red and blue pimpernels (Anagallis arvensis and A. coerulea, which the best botanists rank as mere varieties) and found them to be absolutely sterile, we may doubt whether many species are really as sterile when intercrossed as he believed. Clearly, Gärtnert’s data are not easy to interpret, and probably don’t show what he thinks they show.

On the one hand, it is clear that the sterility of various species when artificially crossed is very different in degree and graduates away insensibly depending on the species studied and, on the other hand, that the fertility of pure species is very easily affected by various circumstances; for all practical purposes, then, it is most difficult to say where perfect fertility ends and sterility begins. I think no better evidence of this can be required than that the two most experienced observers who have ever lived, namely Kölreuter and Gärtnert, should have arrived at diametrically opposite conclusions about
the status (are they species? Or are they merely varieties of a single species?) of the exact same forms. It is similarly instructive to compare—lack of space prevents me from going into detail here—the evidence advanced by our best botanists on the question of whether certain doubtful forms should be ranked as species or varieties with the evidence from fertility adduced either by evidence from different hybridizers, or from evidence provided by the same hybridizer from experiments made during different years. It can thus be shown that neither sterility nor fertility affords any clear distinction between species and varieties. The evidence from this source graduates away, so that tests of sterility are as unclear and as indistinct for defining species as are assessments made from structural and behavioral differences.

Let us consider now the sterility of hybrids in successive generations. Although Gärtner was able to rear some hybrids—carefully guarding them from a cross with either pure parent for six or seven, and in one case for 10 generations—yet he asserts positively that their fertility never increased, but instead generally decreased greatly and suddenly, in keeping with his belief in divinely-endowed mating barriers between species. But I am quite certain that fertility was diminished in nearly all of these cases by too close inbreeding, based on the many experiments that I have conducted and the many facts that I have collected showing, on the one hand, that an occasional cross with a distinct individual or variety increases offspring vigor and fertility, and on the other hand, that very close interbreeding reduces offspring vigor and fertility.

The problem is that hybrids are seldom raised by experimentalists in great numbers; and as the parent species, or other related hybrids, are generally grown in the same garden, the visits of insects must be carefully prevented during the flowering season to avoid unintended cross pollination. Thus hybrids, if left to themselves, will generally be fertilized during each generation by pollen coming from the same flower; this self-fertilization would probably reduce their fertility, which has already been lessened by their hybrid origin. My conviction that this is the case is strengthened by a remarkable
statement repeatedly made by Gärtner, namely that if even the less fertile hybrids are artificially fertilized with hybrid pollen of the same kind, their fertility, notwithstanding the frequent ill effects from manipulation, sometimes increases markedly and goes on increasing. Now I know from my own experience that, in the process of artificial fertilization, pollen is as often taken by chance from the anthers of another flower as from the anthers of the flower that is to be fertilized; a cross between two flowers, though probably often on the same plant, would be thus achieved. Moreover, whenever complicated experiments are in progress, so careful an observer as Gärtner would have castrated his hybrids, and this would have ensured that each generation resulted from a cross using pollen from a different flower, either from the same plant or from another plant of the same hybrid nature. And thus, the strange fact of increased fertility in the successive generations of artificially fertilized hybrids, in contrast with those spontaneously self-fertilized, may be accounted for simply from too close inbreeding having been avoided.

Now let us turn to the results arrived at by another most-experienced hybridizer, namely the Hon. and Rev. W. Herbert. He is just as emphatic in his conclusion that some hybrids are perfectly fertile—as fertile, in fact, as offspring from the pure parent species—as Kölreuter and Gärtner are in their conclusion that some degree of sterility between distinct species is a universal law of nature. Yet Herbert experimented on some of the very same species that Gärtner worked with! The difference in their results may, I think, be explained at least in part by Herbert’s greater horticultural skill, and by his being able to conduct his studies in hot-houses. Of his many important statements I will give here only one example, namely that “every ovule in a pod of Crinum capense fertilized by C. revolutum7 produced a plant, which I never saw to occur in a case of its natural fecundation.” So here we have a perfect, or even more than commonly perfect, fertility in a first cross between two distinct plant species.

In keeping with this case of successful cross-fertilization between two species of Crinum, I must add that individual plants of certain species of Lobelia, Verbascum, and Passiflora, can easily be fertilized
using pollen from plants of a different species, but not by using pollen from the same plant, even though this pollen can be shown to be perfectly sound in that we can successfully fertilize other plants with it. In the plant genera *Hippeastrum* and *Corydalis* (as shown by Professor Hildebrand), and in various orchids (as shown by Mr. Scott and Fritz Müller), all the individuals are in this peculiar condition. So that with some species certain abnormal individuals, and in other species all the individuals, can actually be hybridized with other species much more readily than they can be fertilized by pollen from the same individual plant! To give just one example, a bulb of *Hippeastrum aulicum*—the South American “lily of the palace,”—produced 4 flowers. Herbert fertilized three of those flowers with their own pollen, and the 4th was subsequently fertilized using pollen of a compound hybrid that was descended from three distinct species. 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 pollen of the hybrid made vigorous growth and rapid progress to maturity, and bore good seed, which vegetated freely.” Mr. Herbert tried similar experiments over many years, and always saw the same result. Thus we see on what slight and mysterious causes the lesser or greater fertility of a species sometimes depends.

The practical experiments of horticulturists, though not made with scientific precision, also deserve some notice. It is notorious in how complicated a manner species of *Pelargonium, Fuchsia, Calceolaria, Petunia, Rhododendron*, and many other plants have had to be crossed; and yet many of the resulting hybrids seed freely. For example, Herbert asserts that a hybrid from *Calceolaria integrifolia* and *C. plantaginea*—species that are quite dissimilar in general habit—“reproduces itself as perfectly as if it had been a natural species from the mountains of Chili [Chile].” Similarly, I have taken some pains to ascertain the degree of fertility of some of the complex crosses between various species of rhododendrons, and I am assured that many of them are perfectly fertile. Mr. C. Noble, for example, tells me that he raises stocks for grafting from a hybrid between *Rododendron ponticum* and *R. catawbiense*, and that this hybrid “seeds as freely as it is possible to imagine.” Indeed, had hybrids
when fairly treated always gone on decreasing in fertility with each successive generation, as Gärtner believes to be the case, the fact would have been notorious to nurserymen. Horticulturists raise large beds of the same hybrid, and such alone are fairly treated, for by insect-mediated pollen transfer the several individuals are allowed to cross freely with each other, and the injurious influence of close interbreeding is thus prevented. Any one may readily convince himself of the efficiency of insect-mediated pollen transfer by examining the flowers of the more sterile kinds of hybrid rhododendrons, which produce no pollen, for he will find on their stigmas plenty of pollen brought there from other flowers. Clearly, species are not universally separated from each other reproductively.

Many fewer careful experiments have been tried with animals than with plants. If the genera of animals are as distinct from each other as are the genera of plants, then we may infer that animals more widely distinct in the scale of nature can be crossed more easily than in the case of plants. Although the hybrids themselves seem more likely to be sterile, it should be borne in mind that, owing to few animals breeding freely under confinement, few good experiments have been yet been conducted. For instance, the canary-bird has been crossed with nine distinct finch species, but, as not one of those species breeds freely under confinement, we have no right to expect that the first crosses between them and the canary—or that their hybrids—should be perfectly fertile. Again, with respect to the fertility in successive generations of the more fertile hybrid animals, I hardly know of even a single instance in which two families of the same hybrid have been raised at the same time from different parents, so as to avoid the detrimental effects of close inbreeding⁹. On the contrary, brothers and sisters have usually been crossed in each successive generation, contrary to the constantly repeated admonition against such crosses by every breeder. And with such continued inbreeding it is not at all surprising to find that the inherent sterility in the hybrids should have gone on increasing from generation by generation.

Although I know of hardly any thoroughly well-authenticated cases of perfectly fertile hybrid animals, I have reason to believe that hybrids from the genera *Cervulus* (a genus of small Asiatic deer),
Baginalis, and Reevesii, and from the pheasants Phasianus colchicus with P. toraquatus, are perfectly fertile. The zoologist M. Jean Louis Armand de Quatrefages states that hybrids obtained from matings between two moth species (Bombyx cynthia and B. arrindia) were proved in Paris to be fertile among themselves for eight generations. It has recently been asserted that two such distinct species as the hare and rabbit, when they can be made to breed together, produce offspring that are highly fertile when crossed with one of the parent species. The hybrids resulting from crosses between the common goose and Chinese geese (A. cygnoides), species that differ from each other so greatly that they are generally considered to be members of different genera, have often gone on to successfully breed in this country with either pure parent, and in one case they have bred successfully among themselves. This was achieved by the English naturalist Mr. Thomas Campbell Eyton, who raised two hybrids from the same parents, but from different hatches. And from these two birds he then raised no less than eight hybrids (grandchildren of the pure geese) from one nest. In India, however, these cross-bred geese must be even more fertile, for I am assured by two eminently capable judges—Mr. Blyth and Captain Hutton—that whole stocks of these crossed geese are kept in various parts of the country. And as they are successfully kept for profit, where neither pure parent-species exists, they must certainly be highly, or even perfectly, fertile.

With our domesticated animals, the various races are quite fertile when crossed together; yet, in many cases the members of those races are descended from two or more wild species. From this fact we must conclude either that the original parent-species at first produced perfectly fertile hybrids, or that the hybrids subsequently became fertile when reared under domestication. This latter possibility, which was first suggested by the German botanist and zoologist Peter Simon Pallas, seems the most likely, and can, in fact, hardly be doubted. Thus I have recently acquired decisive evidence that the offspring resulting from crosses between Indian humped cattle and common cattle are perfectly fertile among themselves. Moreover, from the observations of Rütimeyer on their important osteological...
differences, as well as from those by Mr. Blyth on their differences in such characteristics as habits, voice, and constitution, these two forms must be regarded as good and distinct species. The same remarks may be extended to the two chief races of the pig. Thus we have two choices: we must either give up the belief in the universal sterility of species when crossed, or we must look at this sterility in animals, not as an indelible, natural characteristic but rather as one capable of being removed by domestication.

Finally, considering all the known facts concerning intercrossing in plants and animals, we may conclude that although some degree of sterility is an extremely general result, both in first crosses between species and in hybrids, it cannot, as far as we can tell at present, be considered as absolutely universal.

**Laws Governing the Sterility of First Crosses and of Hybrids**

**PREVIEW:** Here, Darwin attempts to generalize from studies on both plants and animals about the rules that determine how successful crosses will be in producing offspring, and in producing offspring that themselves will be capable of reproducing. He comes up with a number of general rules, but shows that there are interesting exceptions to each of them, again suggesting that the reproductive boundaries between species are not absolute. Remarkably, the ability to successfully graft\textsuperscript{11} certain plants onto other plants follows similarly complex patterns. And certainly, Darwin argues, no one has ever suggested that the ability to successfully graft type of plant onto another type of plant is a divinely-endowed characteristic.

Let us consider in a little more detail the laws governing the sterility of first crosses between members of different species and of hybrids. Our chief goal will be to see whether or not these laws indicate that species have been specially endowed with sterility to deliberately prevent them from crossing and
blending together in utter confusion; in other words, to keep all species distinct. **My major point here is to show that although there do seem to be a number of general laws, there are fascinating exceptions to all of them.**

The following conclusions are drawn mainly from Gärtner’s admirable work on hybridization in plants. I have taken great pains to determine how far they apply as well to animals, and considering how limited our knowledge is in regard to hybrid animals, I have been surprised to find how generally the same rules apply to organisms in both kingdoms.

I have already shown in the previous section that the degree of fertility, both of first crosses between members of different species and of hybrids, graduates in different cases from zero in some to perfect fertility in others. It is surprising in how many curious ways this gradation can be shown. But here I can give only the barest outline of the relevant facts. For example, when pollen from a plant belonging to one family is placed on the stigma of a plant from a distinctly different family, it exerts no more influence than so much inorganic dust. In contrast to this complete sterility between such species, the pollen of different species applied to the stigma of some one species of the same genus yields a perfect gradation in the number of seeds produced, up to nearly complete fertility, or even complete fertility—even, as we have seen, in certain abnormal cases, to an excess of fertility beyond that which the plant’s own pollen produces.

And so it is, too, with hybrids themselves: there are some hybrids that never have produced—and probably never would produce, even with the pollen of the pure parents—a single fertile seed. But in some of these cases a first trace of fertility may be detected, by the pollen of the pure parent species causing the flower of the hybrid to wither sooner than it otherwise would have done; the early withering of the flower is well known to be a sign of incipient fertilization. Again, there is a gradient: from an extreme degree of sterility resulting from a cross between species, we have self-sterilized hybrids producing more and more seeds up to perfect fertility.
The hybrids raised from two species that are very difficult to cross, and which rarely produce any offspring, are generally very sterile; that is, they produce no viable gametes. **But the difficulty in making a first cross is not always associated with the sterility of the hybrids thus produced.** There are many cases (the plant genus *Verbascum*, for example) in which even though two pure species can be crossed with unusual facility, producing numerous hybrid offspring, those hybrids are remarkably sterile. On the other hand, there are species that, although they can be successfully crossed only very rarely, or only with extreme difficulty, the hybrids, when at last produced, are themselves very fertile. Indeed we sometimes see these two opposite cases even within the same genus, as in the genus *Dianthus*, a group of about 300 species of flowering plants belonging to the family Caryophyllaceae.

The fertility of first crosses between members of different species also varies considerably among the individuals of those species; sometimes the cross succeeds brilliantly, sometimes only to a degree, and sometimes not at all, depending on the individuals involved. The same is true of crosses among plant hybrids: the degree of fertility often differs greatly even among individuals raised from seeds taken from the same capsule and exposed to the same environmental conditions.

To some extent, the fertility of first crosses, and of the hybrids thus produced, is largely governed by how closely related they are to each other—that is, to their “systematic affinity.” This is clearly shown by the fact that hybrids have never been raised between species that systematists rank as belonging to different families, whereas more closely-related species can usually be mated with success. **But there are many exceptions to this general truth.** I know of many cases in which we have not been able to successfully mate some closely related species, or in which we have been able to do so only with great difficulty. On the other hand, I also know of cases in which the members of very distantly related species have been interbred with ease. Within a single family of plants, for example, there may be one genus—*Dianthus*, for example --- in which very many species can be crossed very easily, while in another genus, such as *Silene*[^15], the most persevering efforts have failed to produce even a single hybrid.
We sometimes see this same sort of difference among species within the same genus. For example, the many species in the tobacco genus *Nicotiana* have been more commonly crossed together than the species of almost any other genus of plants; yet Gärtner found that *N. acuminata*, which is not a particularly distinct species, obstinately refused to be fertilized by, or refused to fertilize, no less than 8 other species in the same genus. Many similar cases could be given.

No one has been able to identify a kind or an amount of difference in any recognizable character that is sufficient to prevent any two species from successfully crossing. Even some plants that differ greatly in habit and general appearance, and which have strongly marked differences in every part of the flower—and even in the pollen, in the fruit, and in the cotyledons—can be readily crossed. And the same is true for many annual and perennial plants, deciduous and evergreen trees, and plants living in very different habitats and exposed to extremely different climates—these can often be crossed with ease.

Let us now consider reciprocal crosses, by which I mean a female of one species being crossed with a male of a different species, and a male of the first species being crossed with a female of the second species—a female donkey (*Equus africanus asinus*) being first crossed with a male horse (a stallion), for example, and then a female horse (a mare) being crossed with a male donkey. Those two species can then be said to have been “reciprocally crossed.” Sometimes it is very easy to make such reciprocal crosses, and sometimes it is extremely difficult...or impossible. Such cases are highly important for us, for they prove that the capacity in any two species to be crossed often has nothing to do with how closely-related they are. Kölreuter has observed a great diversity of results from reciprocal crosses between the same two species in a great number of experiments conducted over many years. For example, he has shown that *Mirabilis jalapa*, the “four o’clock flower” of Peru, can easily be fertilized by the pollen of *M. longiflora*, and that the resulting hybrids are reasonably fertile. The reverse, however, is not true: *M. longiflora* cannot be fertilized by pollen taken from *M. jalapa;
indeed he tried that experiment more than 200 times over 8 years, and failed utterly. The French botanist Gustave Thuret has observed the same results in experiments with certain seaweed species, while Gärtner has observed something similar between even more closely-related forms such as *Matthiola* \textsuperscript{17} *annua* and *M. gilabra*, which most botanists rank as only varieties of a single species. It is also a remarkable and well-known fact that the hybrids raised from successful reciprocal crosses, although of course compounded of the very same two species—the one species having first served as the father and then as the mother—generally differ at least somewhat in fertility, and sometimes to a very high degree, even though they rarely differ in external appearance.

Gärtner has also shown that some plant species can be easily crossed with other species and that some different species within a given genus have a remarkable power of impressing their likeness on their hybrid offspring. **But these two powers do not necessarily go together.** For example, certain hybrids, instead of having characteristics intermediate between those of their two parents, always closely resemble just one of them; and such hybrids, though resembling so closely just one of their pure parent species, are almost always extremely sterile. Similarly, amongst hybrids that are structurally intermediate between their parents, exceptional and abnormal individuals are sometimes born that closely resemble just one of their pure parents. Those hybrids are almost always utterly sterile, even when the other hybrids raised from seeds obtained from the same capsule show a considerable degree of fertility. **These facts show very clearly how the fertility of a hybrid may have little to do with how much it resembles either of its pure parents.**

In summary, we see 1) that when forms that must be considered perfectly good and distinct species are crossed, their fertility graduates from zero to perfect fertility, or even to an excess of fertility under certain conditions, depending on the species involved; 2) that fertility varies considerably among individuals within a species; 3) that the degree of fertility is by no means always the same in the first cross and in the hybrids produced from that cross; 4) that the fertility of hybrids is not related to the
degree to which they resemble either of their parents; and 5) that the ease of making a first cross between individuals of any two species is not necessarily determined by how closely related those species are, or by the degree to which they resemble each other. This latter point (5) is clearly proven by the differences obtained in reciprocal crosses between individuals of the same two species: depending on which species is used as the father and which is used as the mother, there is generally some difference, and occasionally the widest possible difference, in the likelihood of obtaining offspring. Moreover, the hybrids produced from reciprocal crosses between species often differ in fertility, depending on which species served as the mother and which as the father.

Do these complex and singular rules support the contention that species have been deliberately endowed with sterility to prevent their becoming confounded in nature? I think not. For why should the degree of sterility differ so greatly when different species are crossed, when it should be equally important to keep any two species from blending together? And why should the degree of sterility differ among individuals within a species? And why should some species be easy to cross successfully with some other species and yet produce hybrids that are sterile, while other species are extremely difficult to cross successfully and yet produce hybrids that are quite fertile? Why should there often be so great a difference in the result of a reciprocal cross between members of same two species, depending on which species serves as the mother and which as the father? Why, it may even be asked, has the production of hybrids been permitted at all? To grant to some species the special power of producing hybrids and then to stop their further propagation by causing different degrees of sterility in those hybrids, degrees that are not related to how easy it was to obtain a successful mating between the parents in the first place, seems a very strange arrangement indeed.

It seems quite clear to me from the forgoing facts that the degree of sterility both of first crosses between species and of the hybrids produced from such crosses must be caused by some unknown differences in their reproductive systems, not by any “design” to keep the species separated. Whatever
the causes are, they are clearly of a peculiar and limited nature such that in reciprocal crosses between two species, the male sexual element of the one species will often successfully interact with the female element of the other species, while the male element of that second species cannot successfully fertilize the eggs of the first species.

Let me explain through another example—something called “grafting”¹⁸—what I mean by sterility being caused by “unknown differences” in the reproductive systems, and not by any specially endowed quality. Our ability to successfully graft one plant onto another has no role in determining their subsequent welfare in nature; thus I presume that no one will suppose that this capacity is “specially endowed,” but will rather admit that it has something to do with differences in the laws of growth in the two plants. We can sometimes see why one type of tree cannot be grafted onto another from differences in their rates of growth, or in the hardness of their wood, or in the period of the flow or the nature of their sap, and so forth. But in a multitude of cases we can assign no reason whatsoever. Great diversity in the sizes of two plants, or one plant being woody and the other herbaceous, or one being evergreen and the other deciduous¹⁹, or adaptation to very different climates—none of those things will always prevent the two from being successfully grafted together. **As with hybridization, so it is with grafting: the capacity for successful grafting depends on degrees of relatedness, e.g., “systematic affinity.”** For no one has been able to graft together trees belonging to quite distinct families, whereas closely related species, and varieties of the same species, can usually—but not invariably—be grafted with ease.

**But this capacity for grafting, as in hybridization, is by no means absolutely determined by systematic affinity.** Although members of many distinct genera within a single family have been successfully grafted together, there are also some species within a single genus that will not take each other on. Indeed, the pear can be grafted far more readily onto the quince, which is ranked as belonging to a different genus, than onto the apple, which belongs to the same genus²⁰. Even different
varieties of the pear take on the quince with different degrees of facility, and the same is true with
different varieties of the apricot and peach on certain varieties of the plum.

Just as Gärtner has found that there was sometimes an innate difference in the ability of
different *individuals* within the same two species to cross successfully, so the French botanist Sageret
believes this to be the case with different individuals of the same two species in being successfully
grafted together. Just as the ease of achieving a union is often very far from equal in reciprocal crosses
between species, so it sometimes is in grafting: the common gooseberry, for instance, *cannot* be grafted
on to the currant, whereas the currant *can* be grafted onto the gooseberry, though admittedly only with
difficulty.

We have seen that the sterility of hybrids, which have their reproductive organs in an imperfect
condition, is a quite different issue from the difficulty of uniting two pure species, which of course have
their reproductive organs perfectly well developed and fully functional. And yet, these two distinct
classes of cases run to a large extent parallel. Something analogous occurs with grafting. The French
botanist André Thouin, for example, found that although three species in the deciduous plant genus
*Robinia* that seeded freely when growing attached to their own roots could be grafted easily onto a 4th
*Robinia* species, those grafts were unable to produce seed. On the other hand, certain species of trees
and shrubs in the genus *Sorbus* (which belong to the rose family Rosaceae, along with the pears,
quinces, and apples mentioned earlier) produced twice as much fruit when grafted onto other species as
when they were left attached to their own roots. This latter result reminds us of the extraordinary cases
of *Hippeastrum*, *Passiflora*, and some other plants, which seeded much more freely when fertilized with
the pollen of a different species than when fertilized with pollen from the same plant.

Thus we see that there is a certain degree of parallelism in the results from grafting and of the
crossing of distinct plant species. And as we must look at the curious and complex laws governing the
ease with which trees can be successfully grafted onto each other as depending on some unknown
differences in their vegetative systems, so I believe that the still more complex laws that must govern the ability to make successful first crosses between the members of different species must also depend on unknown differences in their reproductive systems. To some extent these differences are related to degrees of systematic affinity. But the facts that we have here discussed by no means seem to support the idea that the greater or lesser difficulty of either grafting or crossing various species has been a “special endowment” of divine creation.

**The Origin and Causes of the Sterility of First Crosses and Hybrids**

PREVIEW: If sterility is not universal and divinely endowed, then how do we explain it? Here Darwin uses the limited evidence available at the time to try to figure out what causes sterility, how it might have originated, and whether it may have originated through natural selection or in some other way. But the causes ultimately remain, for Darwin, unfathomable, since he knew nothing about chromosomes or genes.

Many crosses between different species fail to produce offspring. And of those that do produce offspring, the hybrids are often completely sterile. At one time it seemed likely to me, as it has to others, that this sterility of first crosses and of hybrids might have been something that was slowly acquired through the natural selection of slightly lessened degrees of fertility in each generation, when such variations appeared in certain individuals of one variety when crossed with those of another variety. It would clearly be advantageous to two varieties if they could be kept from blending, for the same reason that when breeders are selecting for two varieties of plant at the same time, they must keep the plants well separated to prevent unwanted crossing.

After mature reflection, however, it now seems to me that in most cases, sterility could not have been achieved through natural selection. For example, take the case of any two species which,
when crossed, produced few and sterile offspring. What could favor the survival of those individuals that happened to be endowed in a slightly higher degree with mutual infertility, and which thus approached towards absolute sterility by this one small step? We have already seen (see Chapter 8, The Readable Darwin) that modifications in the structure and fertility of what are now sterile neuter insects probably did in fact come about slowly, over many generations, through natural selection, from an advantage having been thus indirectly gained by the community to which those individuals belonged over other communities of the same species. But an individual animal not belonging to a social community, if rendered slightly sterile when crossed with some other variety, would not thereby gain any advantage for itself, and would not indirectly give any advantage to other individuals of the same variety; so nothing would lead to their preservation. The sterility seen among so many crossed species must have a basis in something other than natural selection, but we cannot at present say what that basis is.22

Let us now look more closely at the factors that likely account for the sterility seen in so many first crosses and in hybrids. In the case of first crosses between the members of different species, the degree of difficulty in achieving a union of gametes and in obtaining offspring apparently depends on several distinct causes. Among plants, sometimes there is something that just physically prevents the male gamete (pollen) from reaching the ovule.23 Such would be the case, for example, with a plant having a pistil that is too long for the pollen-tubes from another plant to reach the ovarium.24 It has also been observed that when the pollen of one species is deliberately placed on the stigma of a distantly related species, although the pollen-tubes protrude, they do not—for some reason—succeed in penetrating the surface of the stigma.

Alternatively, the male gamete may reach the female gamete but for unknown reasons be incapable of causing an embryo to be developed, as seems to have been the case in some of Gustave Thuret’s experiments on seaweeds. Lastly, an embryo may start to develop after fertilization but then
perish shortly afterwards. This situation has not been sufficiently studied, but I believe, based on observations communicated to me by Mr. Edward Hewitt, someone who has had a great deal of experience in hybridizing both pheasants and fowls, that the early death of the embryo is a very frequent cause of sterility in first crosses. Indeed, Mr. Salter has recently reported the results of his studies on about 500 eggs produced from various crosses between three species of birds in the genus Gallus and their hybrids. Most of the eggs he examined had been fertilized. However, in many of those eggs the embryos had developed only partially before perishing, and in many other egg, although the embryos had matured nicely, the young chickens had then been unable to break through the egg shell and had died without hatching. Of the few chickens that successfully hatched, more than 80% died within the first few days, or in later weeks, “without any obvious cause, apparently from mere inability to live.” Thus of the 500 eggs that he worked with, only 12 chickens could be reared.

And so it is with plants, with hybridized embryos probably often perishing in a similar manner. Certainly we know that even when fertilization is successful, hybrids raised from very distinct species are sometimes weak and dwarfed, and perish at an early age. Indeed, the German botanist Max Ernest Wichura has recently given some striking cases with hybrid willows. It may also be worth noting here that in some cases of parthenogenesis, the embryos of silk moths from eggs that had not been fertilized pass through their early development but then perish, just like the embryos produced from a cross between distinct species. The cause is as yet unknown.

Indeed, there are many facts about the sterility of hybrids that are still beyond our understanding. For instance, how can we explain the unequal fertility of hybrids produced from reciprocal crosses, or the increased sterility in those hybrids that occasionally and exceptionally resemble closely either pure parent? All of these facts seem connected by some common but unknown bond, something that must be related to some great principle of life that remains to be uncovered.
Reciprocal Dimorphism and Trimorphism

PREVIEW: Some plant species produce two or three distinctly different forms of flower within a single variety. Remarkably, fertility varies with the form of flower used to provide the pollen or egg, showing, in fact, just the sort of variability in fertility that we see among varieties and species. Note that this section was not included in the 1st edition of The Origin—or even in the 3rd edition; it appears for the first time in the 4th edition, which appeared June 1866.

This topic will throw some light on the degree of sterility brought on by hybridism. Several plants belonging to distinctly different orders present two distinct forms of flower that exist in about equal numbers and that differ only in their reproductive organs: one form of flower has a long pistil with short stamens, while the other has a short pistil and long stamens (See Figure 7.1, p 187 in Volume 1 of The Readable Darwin); the two also differ in the size of the pollen grains produced. With “trimorphic” species, there are three flower forms that likewise differ in the lengths of the pistils and stamens, in the size and color of the pollen grains, and in some other respects as well; as there are two sets of stamens in each of the three forms, the three forms possess altogether six sets of stamens and three kinds of pistils. These organs are proportioned in length relative to each other such that half of the stamens in two of the forms stand at the same level as the stigma of the third form. Now I have shown—and my results have been since confirmed by other observers—that in order to obtain full fertility with these plants, one must be sure that the stigma of the one form should be fertilized by pollen taken from the stamens of corresponding height in another form; i.e., the pollen from a long stamen must contact a long pistil on another flower, and the pollen from a short stamen must contact a short pistil on another flower. Thus with dimorphic plant species, two unions (which I will call “legitimate” unions) are fully fertile, and two other unions (which I will call “illegitimate” unions) are infertile to some degree. With
trimorphic species, six unions will be legitimate, or fully fertile, and 12 will be illegitimate, or more or less infertile.

The degree of infertility that may be observed in various dimorphic and trimorphic plants of a single species when their flowers are fertilized by pollen taken from stamens not corresponding in height with that of the pistil (i.e., illegitimate fertilization) differs much in extent, from only small reductions in reproductive potential in some cases to utter sterility in others, just as we have seen happening when the members of distinct species are crossed.

It is well known that if pollen from one flower of a particular species is placed on the stigma of a flower of a different species, and the pollen of that second species is afterwards—even after a considerable interval of time—placed on the same stigma of the same flower, its action is so strongly pre-potent that it generally annihilates the effect of the foreign pollen. And so it is with the pollen of the several forms of the same species, for legitimate pollen is strongly pre-potent over illegitimate pollen when both are placed on the same stigma. I discovered this myself by fertilizing several flowers, first illegitimately and then legitimately 24 h later, using pollen taken from a peculiarly colored variety. All the seedlings that were eventually produced were similarly colored, showing that the legitimate pollen, although applied 24 h after the illegitimate pollen, had wholly destroyed or in some other way prevented the successful action of the previously applied illegitimate pollen. Again, as in making reciprocal crosses between the same two species, there is occasionally a great difference in results. The same thing occurs with trimorphic plants\textsuperscript{27}: for instance, the mid-styled form of purple loosestrife (\textit{Lythrum salicaria}) was illegitimately fertilized with the greatest ease using pollen from the longer stamens of the short-styled form, and yielded many seeds; but the latter form did not yield a single seed when fertilized with pollen from the longer stamens of the mid-style form.

In all these respects, the different forms of the same undoubted species of dimorphic or trimorphic plant when illegitimately united, behave in exactly the same manner as do two distinct
species when crossed. This led me to carefully observe, for four years, many seedlings that I raised from several illegitimate unions. The chief result is that these “illegitimate” plants were never fully fertile. It is possible to raise both long-styled and short-styled illegitimate plants from dimorphic species, and to raise all three illegitimate forms from trimorphic plants. These can then be properly united in a legitimate manner; i.e, the pollen from a long stamen is used on a plant with a long pistil, and the pollen from a short stamen is used on a plant with a short pistil. When this is done, there is no apparent reason why they should not yield as many seeds as did their parents when legitimately fertilized. But such is not the case! In my experiments, they were all infertile to various degrees, some being so utterly and incurably sterile that they did not yield a single seed or even a seed-capsule during my 4 seasons of study.

The sterility of these illegitimate plants when united with each other in a legitimate manner is exactly comparable to the sterility of hybrids when crossed amongst themselves. If, on the other hand, a hybrid is crossed with either pure parent-species, the degree of sterility is usually reduced considerably. The same holds true when an illegitimate plant is fertilized using pollen from a legitimate plant. Similarly, in the same way that the degree of sterility of hybrids does not always correspond with the degree of difficulty in making the first cross between the two parent species, so it is that the sterility of certain illegitimate plants was unusually great while the sterility of the union from which they were derived was not great. Moreover, the degree of sterility varies from seed to seed with hybrids raised from the same seed-capsule, and the same is markedly true with illegitimate plants. Lastly, many hybrids are profuse and persistent flowerers, while other, more sterile hybrids produce few flowers and are weak, miserable dwarfs; exactly similar cases occur with the illegitimate offspring of various dimorphic and trimorphic plants.

Taken together, there is a marked parallel between the character and behavior of illegitimate plants and the hybrids resulting from crosses between members of different species. It is hardly an
exaggeration to maintain that illegitimate plants are essentially hybrids, produced within the limits of
the same species by the improper union of certain flower forms, whilst ordinary hybrids are produced
from an improper union between so-called distinct species.

We have also seen previously that there is the closest similarity in all respects between first
illegitimate unions and first crosses between the members of distinct species. Allow me to illustrate.
Suppose that a botanist found two well-marked varieties of the long-styled form of the trimorphic plant
Lythrum salicaria (purple loosestrife, as mentioned earlier)—and such varieties do in fact exist—and that
he wanted to determine by crossing whether they were actually different species. But to make the case
sure, he would then raise the plants grown from his supposedly hybridized seed, and he would find that
the seedlings were miserably dwarfed and utterly sterile, and that they behaved in all other respects like
ordinary hybrids. He might then maintain that he had actually proven that his two varieties were as
good and as distinct species as any in the world. But of course he would be completely mistaken in
taking this view.

These facts about degrees of sterility in dimorphic and trimorphic plants are important because,
for one thing, they show us that the physiological test of lessened fertility, both in first crosses and in
hybrids, is no safe criterion for defining species. They also suggest that there is some unknown bond
that connects the infertility of illegitimate unions with that of their illegitimate offspring, leading us to
extend the same view to first crosses and hybrids. Also, these facts show that there can be two or three
forms of the same species that are sterile when united in certain ways, even though they don’t differ at
all in either structure or constitution. Remember that it is the union of the sexual elements of
individuals of the same form—two long-styled forms, for example—that results in sterility, while it is the
union of the sexual elements proper to two distinct forms that is fertile. Hence the case appears at first
sight exactly the reverse of what occurs in the ordinary unions of the individuals of the same species and
with crosses between distinct species. It is, however, doubtful whether this is really so; but I will not
enlarge on this obscure subject here. We may infer, however, from our consideration of dimorphic and trimorphic plants, that the sterility of distinct species when crossed (and of their hybrid offspring) depends exclusively on the nature of their sexual elements, and not on any difference in their structure or general constitution. We are led to the same conclusion by considering reciprocal crosses, in which the male of one species cannot be united, or can be united only with great difficulty, with the female of a second species, whilst the converse cross can be achieved with ease. That excellent observer Gärtner similarly concluded that species when crossed are sterile owing to differences confined to aspects of their reproductive systems. We have yet to understand just what those aspects are.

**The Fertility of Varieties When Crossed, and of Their Mongrel Offspring, Is Not Universal**

PREVIEW: Although varieties of any particular species can usually be successfully mated with each other, resulting in viable offspring that are themselves capable of eventually mating, that turns out to not always be the case. Here Darwin provides several such exceptions, all from botanical experiments. In a number of cases, for example, it has proven surprisingly difficult to obtain viable offspring from matings between different varieties of the same species. And varieties of a given species can also differ in the degree to which they can be successfully mated with members of a different species.

It may be strongly argued that there must be some essential distinction between species and varieties, inasmuch as varieties, however much they may differ from each other in external appearance, may usually be crossed with ease and yield perfectly fertile offspring. I fully admit that this is generally the case. But the evidence often involves circular reasoning: looking at varieties produced in nature, if two forms previously said to be varieties of a species are found to be sterile with each other to any degree,
they are at once ranked by most naturalists as distinct species! For example, the blue and red pimpernel (flowers belonging to the genus *Anagallis*), which most botanists consider to be separate varieties, are said by Gärtner to be quite sterile when crossed; thus he now ranks them with conviction as undoubted separate species of that genus\(^3\). With that sort of circular reasoning, the fertility of all varieties produced in nature will assuredly have to be granted.

Let us turn now to varieties that we believe were produced under domestication. The perfect fertility of so many domestic races when crossed—as with the various breeds of pigeons (see Chapter 1 of *The Readable Darwin*), or dogs, or cabbages, for example—is a remarkable fact, considering how much they differ in physical appearance. This is especially remarkable considering how many species we know of that are utterly sterile when crossed even though they resemble each other quite closely. The main issue here is not, I think, why domestic varieties have not become mutually infertile when crossed, but why this has so generally occurred with *natural* varieties, as soon as they have been permanently modified in a sufficient degree to take rank as species. We are far from understanding the cause, something that should not be particularly surprising, seeing how profoundly ignorant we are in regard to the normal and abnormal action of the reproductive system.

Although varieties of a given species are usually fertile when intercrossed, it is impossible to resist the evidence of a certain amount of sterility occurring in at least a few cases, which I will briefly summarize. The evidence for sterility here is at least as good as that from which we believe in the sterility of crosses between a multitude of species. It is also worth noting that the evidence I am about to present is derived from hostile witnesses, who in all other cases consider fertility and sterility to be safe criteria for defining species.

First, for several years Carl Friedrich von Gärtner kept in his garden, growing near to each other, two varieties of maize: a dwarf kind of maize with yellow seeds and a tall variety with red seeds. Both have separated sexes, and they never naturally crossed. He then attempted to fertilize 13 flowers of the
one kind with pollen taken from the other; only a single head produced any seeds, and this one head produced only 5 grains. [Note that the manipulation involved in obtaining the pollen and effecting fertilization could not have been injurious here, as the plants have separated sexes] No one, I believe, has ever thought these varieties of maize to be distinct species, and it is important to note that the hybrid plants thus raised were themselves perfectly fertile. Thus even Gärtner did not consider the two varieties to actually be distinct species, despite the massive failure of 12 of the 13 crosses, and the limited success of the 13th. Clearly, varieties of a given species are not always interfertile.

Similarly, Girou de Buzareingues, a well-known French expert in plant physiology and agronomy, crossed 3 varieties of gourd, which like the maize has separate sexes. He asserts, in his 1833 paper, that the degree of their mutual fertilization was less as the differences between them were greater. How far we may trust these experiments I know not; but the forms he experimented on are ranked by the French botanical authority Augustin Sagaret (who mainly bases his classification on the test of infertility) as varieties; the French botanist Charles Victor Naudin has come to the same conclusion. So why does the degree of fertility among acknowledged varieties vary with the degree of dissimilarity in form?

The following case is far more remarkable, and seems at first incredible. But it is the result of an astonishing number of experiments made during many years on nine species of Verbascum, by so good an observer, and so hostile a witness, as Gärtner. He found that the tallow and white varieties when crossed produced less seed than when the similarly colored varieties of the same species were crossed. Moreover, he asserts that when yellow and white varieties of one species were crossed with yellow and white varieties of a different species, more seed was produced by the crosses between the similarly colored flowers than between those which were differently colored. Mr Scott has also experimented with the various species and varieties of Verbascum and although he was unable to confirm Gärtner’s results on the crossing of the distinct species, he found that the differently-colored varieties of the same
species did indeed yield fewer seeds when crossed than did crosses between the similarly colored varieties, in the proportion of 86 to 100. And yet these varieties differ only in the color of their flowers. Indeed, one variety can sometimes be raised from the seed of another.

The German botanist Joseph Köreuter, whose accuracy has been confirmed by every subsequent observer, has experimented on five forms of tobacco plant (genus *Nicotiana*) that are commonly reputed to be varieties, and which he tested by the severest trial—namely by reciprocal crosses. He found their mongrel offspring to be perfectly fertile. But one of these five varieties, when used either as the father or as the mother in being crossed with a different species in the same genus (*Nicotiana glutinosa*), always yielded hybrids that were less sterile than those produced when the 4 other varieties were crossed with *N. glutinosa*. Thus the reproductive system of this one variety must have differed in some manner from that of the others. In any event, he has proven the remarkable fact that one particular variety of common tobacco was more fertile than 4 other varieties when crossed with a widely distinct species of the same genus.

From these facts one can clearly no longer assert that varieties are always fertile when crossed. We have, of course, great difficulty in ascertaining the infertility of varieties in nature, for a supposed variety, if proved to be infertile to any degree, would almost universally be ranked as a distinct species. It does seem, however, that fertility does not constitute a fundamental distinction between varieties and species. The general sterility of crossed species may safely be looked at, not as a special acquirement or endowment, but rather as being incidental, and caused by changes of an unknown nature in their sexual elements.

*Hybrids and Mongrels Compared, Independently of Their Fertility*

PREVIEW: As defined here, “hybrids” result from successful crosses between individuals of different species, while “mongrels” result from crosses between different varieties of a single species. In this, the final subsection of
Chapter 9, Darwin presents evidence that there are no consistently clear distinctions between the performance of hybrids and mongrels. The evidence adds additional support to the idea that different species original as varieties within an ancestral species, that species are basically just especially well-defined varieties.

Independently of the question of fertility, the offspring of species and of varieties when crossed may be compared in several other respects. Gärtner, who so strongly wished to be able to draw a distinct line between species and varieties, could find very few, and, as it seems to me, quite unimportant differences between the so-called “hybrid” offspring of species and the so-called “mongrel” offspring of varieties. Indeed, they agree most closely in many important respects.

I shall here discuss this subject with extreme brevity. The most important distinction is that in the first generation, the offspring of crossed varieties—so-called “mongrels”—vary more than the offspring of crossed species (“hybrids”); but Gärtner admits that hybrids derived from species that have been cultivated over many generations are often variable in the first generation, and I have myself seen striking instances of this fact. Gärtner further admits that hybrids between very closely allied species are more variable than those from very distinct species; and this shows that the difference in the degree of variability graduates away. When mongrels and the more fertile hybrids are propagated for several generations, an extreme amount of variability in the offspring in both cases is notorious; but in some few instances that have been reported, both hybrids and mongrels long retain a uniform character. The variability, however, in the successive generations of mongrels is, perhaps, greater than it is in hybrids.

Continuing our comparison of mongrels and hybrids, Gärtner states that mongrels are more liable than hybrids to revert to either parent form; but this, if it be true, is certainly only a difference in degree. Moreover, Gärtner expressly states that the hybrids from long cultivated plants are more subject to reversion than hybrids from species in their natural state. This probably explains the singular difference in the results arrived at by different observers. Thus the German botanist Max Ernest Wichura, who experimented on uncultivated species of willows, doubts whether hybrids ever revert to
their parent forms in successive generations, while the French botanist Charles Victor Naudin, who on the other hand, experimented chiefly on cultivated plants, insists in the strongest terms on the almost universal tendency to reversion in hybrids. Gärtner further states that when any two species, even when most closely allied to each other, are crossed with a third species, the hybrids are widely different from each other; but if two very distinct varieties of one species are crossed with another species, the hybrids do not differ much. But this conclusion, as far as I can make out, is founded on a single experiment and seems directly opposed to the results of several experiments made some years ago by Köhlreuter.

These trivial differences are the only differences that Gärtner has been able to point out between hybrid and mongrel plants. On the other hand, the degrees and kinds of resemblance in mongrels and in hybrids to their respective parents, more especially in hybrids produced from nearly related species, follow, according to Gärtner, the same laws. When two species are crossed, one has sometimes a pre-potent power of impressing its likeness on the hybrid. So I believe it to be with varieties of plants; and with animals, one variety certainly often has this pre-potent power over another variety. Hybrid plants produced from a reciprocal cross generally resemble each other closely, and so it is with mongrel plants from a reciprocal cross. Both hybrids and mongrels can be reduced to either pure parent form, by repeated crosses in successive generations with either parent.

These several remarks are apparently also applicable to animals; but the subject is here much complicated, partly owing to the existence of secondary sexual characters, but more especially owing to pre-potency in transmitting likeness running more strongly in one sex than in the other, both when one species is crossed with another species and when one variety is crossed with another variety. For instance, I think those authors are correct when they insist that the donkey (the “ass,” Equus africanus asinus) has a pre-potent power over the horse, so that both the mule and the hinny resemble the donkey more closely than the horse. But this pre-potency runs more strongly in the male donkey than
in the female donkey, so that the mule, which results from mating a male donkey with a mare, is more like a donkey than is the hinny, which results from crossing a female donkey with a stallion.

Much stress has been laid by some authors on the supposed fact that it is only with mongrels that the offspring are not intermediate in character, but closely resemble one of their parents; but this also occurs sometimes with hybrids, although I admit that this occurs much less frequently than with mongrels. Looking to the cases that I have collected of cross-bred animals closely resembling one of the parents, the resemblances seem chiefly confined to characters almost monstrous in their nature, and which have suddenly appeared--such as albinism, melanism, deficiency of tail or horns, or additional fingers and toes; they do not relate to characters that have been slowly acquired through selection. A tendency to sudden reversions to the perfect character of either parent would, also, be much more likely to occur with mongrels, which are descended from varieties often suddenly produced and semi-monstrous in character, than with hybrids, which are descended from species slowly and naturally produced. On the whole, I entirely agree with Dr. Prosper Lucas, an expert in studies of heredity, who, after arranging an enormous body of facts with respect to animals, comes to the conclusion that the laws of resemblance of the child to its parents are the same whether the two parents differ little or much from each other, namely, in the union of individuals of the same variety, or of different varieties, or of distinct species.

Independently of the question of fertility and sterility, in all other respects there seems to be a general and close similarity in the offspring of crossed species, and of crossed varieties. If we look at species as having been specially created, and at varieties as having been produced by secondary laws, this similarity would be an astonishing fact. But it harmonizes perfectly with the view that there is no essential distinction between species and varieties.

Chapter Summary
First crosses between forms that are sufficiently distinct to be ranked as species, and their hybrids, are very generally, but not universally, sterile. Sterility varies widely in degree, and is often so slight that the most careful experimentalists have arrived at diametrically opposite conclusions in ranking forms as being either separate species or varieties of a single species by this test. The sterility is innately variable among individuals of the same species, and is eminently susceptible to action of favorable and unfavorable conditions. The degree of sterility does not strictly follow systematic affinity but is governed by several curious and complex laws. It is generally different—and sometimes widely different—in reciprocal crosses between the same two species. It is not always equal in degree in a first cross and in the hybrids produced from this cross.

In the same manner as in grafting trees, where the ability of one species or variety to take on another depends on differences, generally of an unknown nature, in their vegetative systems, so in crossing, the greater or less facility of one species to unite with another is incidental on unknown differences in their reproductive systems. There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent their crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent their inarching in our forests.

The sterility of first crosses and of their hybrid progeny has not been acquired through natural selection. In the case of first crosses it seems to depend on several circumstances; in some instances in chief part on the early death of the embryo. In the case of hybrids, it apparently depends on their whole organization having been disturbed by being compounded from two distinct forms, the sterility being closely allied to that which so frequently affects pure species when exposed to new and unnatural conditions of life. He who will explain these latter cases will be able to explain the sterility of hybrids. The facts given on the sterility of the illegitimate unions of dimorphic and trimorphic plants, and of their illegitimate progeny, perhaps render it probable that some unknown bond in all cases connects the
degree of fertility of first unions with that of their offspring. The consideration of these facts on
dimorphism, as well as of the results of reciprocal crosses, clearly leads to the conclusion that the
primary cause of the sterility of crossed species is confined to differences in their sexual elements. But
why, in the case of distinct species, the sexual elements should so generally have become more or less
modified, leading to their mutual infertility, we do not know; but it seems to stand in some close
relation to species having been exposed for long periods of time to nearly uniform conditions of life.

It is not surprising that the difficulty in crossing any two species, and the sterility of their hybrid
offspring, should in most cases correspond, even if due to distinct causes, for both depend on the
amount of difference between the species that are crossed. Nor is it surprising that the facility of
effecting a first cross and the fertility of the hybrids thus produced, and the capacity of being grafted
together—though this latter capacity evidently depends on widely different circumstances—should all
run, to a certain extent, in parallel with the systematic affinity of the forms subjected to experiment; for
systematic affinity includes resemblances of all kinds. First crosses between forms known to be
varieties, or sufficiently alike to be considered as varieties, and their mongrel offspring, are very
generally, but not, as is so often stated, invariably fertile. Nor is this almost universal and perfect fertility
surprising, when it is remembered how liable we are to argue in a circle with respect to varieties in a
state of nature, and when we remember that the greater number of varieties have been produced
under domestication by the selection of mere external differences.

Independently of the question of fertility, in all other respects there is the closest general
resemblance between hybrids and mongrels: in their variability, in their power of absorbing each
other by repeated crosses, and in their inheritance of characters from both parent-forms. Finally,
then, although we are as ignorant of the precise cause of the sterility of first crosses and of hybrids as
we are about why animals and plants removed from their natural conditions become sterile, yet the
facts given in this chapter seem fully consistent with the belief that species originally existed as varieties.

Footnotes for Chapter 9 Hybridism

1. Here, sterility means the inability of gametes to combine successfully and produce viable offspring.

2. Hybrids are offspring from a mating between the members of two different species.

3. Mongrels = offspring resulting from matings (“crosses”) between different varieties of a single species.

4. Note that Darwin ignores the role of behavioral isolating mechanisms (e.g., female choice and the timing of sexual activity) in promoting or deterring matings between different species; instead he focuses on forced matings and post-zygotic interactions. His point was that there are no well-defined and absolute reproductive barriers between species, and that species are essentially just varieties that have become increasing different from each other over time.

5. Here Darwin refers to a famous Greek legend involving Alexander the Great, in which a seemingly intractable problem is essentially solved by cheating.

6. Matings between close relatives; we generally now call this “inbreeding.”

7. Both are South African herbaceous plants belonging to the genus *Crinum*.

8. Members of this genus are commonly referred to as “lady’s purse, slipper flower, slipper wort, or pocket book flower”.

9. Matings between close relatives.

10. The branch of vertebrate anatomy dealing with bones.
11. Grafting is a horticultural technique in which tissues from one plant are inserted into those of another, providing an opportunity for the two sets of vascular tissues to join together. In this way, many commercially important plants can be propagated in large numbers asexually.

12. The stigma is the organ containing the ovary. See Figure 7.1 in *The Readable Darwin*, p 187.

13. Species within a single genus are more closely related than are species in different genera within the same family.

14. This group includes the carnation.

15. A very large genus of plants (about 700 species); both *Dianthus* and *Silene* are members of the family Caryophyllaceae.

16. Cotyledons are the embryonic first leaves that develop within plants seeds.

17. A genus of flowering plants in the mustard family, containing about 50 species.

18. As noted earlier, grafting is a horticultural technique in which tissues from one plant are inserted into those of another, providing an opportunity for the two sets of vascular tissues to join together. In this way, many commercially important plants can be propagated in large numbers asexually.

19. “Deciduous” trees and shrubs shed their leaves once each year.

20. Actually, the quince and the apple are now placed in separate genera; the apple belongs to the genus *Mallus*, while the quince is the sole member of the genus *Cydonia*. Both are members of the rose family, Rosaceae, which also contains pears, cherries, plums, and a variety of other fruits. The family contains at least 3,000 species.
21. I have omitted much of this section, as Darwin’s reasoning was severely limited by the fact that he knew nothing about the mechanisms of inheritance, something that must have been terribly frustrating for him.

22. We now know that the sterility of hybrids resulting from crosses between different species (crosses between horses and donkeys, for example) can be caused by the two species having different numbers of chromosomes. In Darwin’s day, of course, chromosomes had not yet been discovered, nor had DNA. The term “chromosome” was first used to describe these cellular components in 1888, by the German anatomist Henrich von Waldyer-Hartz, and were finally recognized as the vectors of heredity in 1902, through the experiments of Theodor Boveri.

23. The ovule is the part of the female plant that contains the egg and eventually becomes the seed, after the egg is fertilized. See Figure 7.1 in Volume 1 of The Readable Darwin.

24. When pollen lands on a stigma, it must “tunnel” into the stigma in order to reach the ovary; if these “pollen tubes” do not form properly the pollen never reaches the eggs.

25. Known as Indian or Red Junglefowl, this genus also includes our domesticated chickens.

26. Parthenogenesis—a form of asexual reproduction, occurring in the absence of fertilization.

27. With trimorphic plants, the reproductive systems come in three different forms, including three differences in the lengths of their pistils (the female part of the flower) and three differences in the lengths of their stamens (the male, pollen-producing part of the flower).

28. Seed capsules are a type of simple, dry fruit produced by many species of flowering plants.
29. Darwin is pretty much on target here; without really knowing it, he is really talking about genetic differences.

30. Indeed, the blue pimpernel plant is now placed in a different genus, the genus *Lysimachia*.

31. *Verbasum* is a member of the snapdragon family

32. Gärtner crossed more than 1,000 flowers in his experiments, and documented the results over a period of 18 years, counting an unimaginable number of seeds in the process!

33. Here Darwin is talking about what we now call “dominance.”

34. A mule results from a cross between a female horse (a mare) and a male donkey, while a hinny results from a cross between a male horse (a stallion) and a female donkey. Both mules and hinnys are generally sterile, because their parents have different numbers of chromosomes. Donkeys, by the way, are basically domesticated horses; both belong to the same family, *Equus*.

35. “Inarching” is a type of grafting in which two plants are grafted together while remaining on their own roots; one plant is later severed from its roots after the graft has been successful.