INTRODUCTION

The Florentine Bizzaria

In 1674, a plant that should never have existed appeared on the outskirts of Florence. The aptly named "Florentine Bizzaria" was a hybrid being (fig. 1). It had been made by grafting—the physical joining of one organism's tissue to that of another—a Florentine citron and a sour orange.[1] Accounts of why the Florentine gardener Pietro Nati had chosen to cross the boundaries between species are varied and contradictory, although at least one held that his foray into transspecies engineering was a mistake.[2] The plant itself certainly looked poorly designed. If you cut into its fruits and dared to taste them, you would find that some segments were bitter, while others tasted of orange. Although it sounds like a remarkable plant, the arrival of the Bizzaria in seventeenth-century Florence probably had little impact upon the city's populace. The idea that new plants could be created through grafting was commonplace in early modern Europe, although questions remained over their true nature.[3] Many accounts of the Florentine Bizzaria instead date to the early twentieth century, when the claim that hybrid organisms could be made by grafting attracted intense scrutiny. As one participant in the scientific debates over these "graft hybrids" would explain, the revived interest of his contemporaries in artificially conjoined plants and animals was "no doubt in association with the revival in that of genetics brought about by the 'rediscovery' of Mendel's work."[4]

Plant grafting is generally performed by attaching a branch (scion) of one plant to the stem (stock) of another. In horticulture, its primary purpose is to propagate plants. By attaching several scions of one plant to the stock of another, you are essentially "cloning" the former.[5] This operation can also combine useful characteristics from different plant varieties. When the French wine industry faced a devastating insect pest in the mid-nineteenth century, botanists found that grafting French grapevines onto resistant rootstock from North America, where the insects had originated, could save the crop. This solution was not without some controversy, as French vineyard owners were concerned that the "inferior" flavor of American wine might seep across the barrier between the plants (a site known as the "graft junction") and pollute their grapes. Eventually, this grafting became the norm and was even celebrated.[6] As the twentieth century dawned, however, grafting came under increased scrutiny from biologists. They had almost the same concern that the French viticulturists had, in that they wished to know whether grafted plants could exchange characters—ranging from disease resistance to fruit color—across the graft junction. Nor were they limited to grafting only plants. Surgical advances meant that organs could be transplanted between farm or laboratory animals. If characters could be swapped between organisms to create hybrids, which in turn could pass these mixed characters on to their offspring, it would transform how twentieth-century biologists understood heredity and open new economic possibilities for agriculture.

This book is about the graft hybrid and its turbulent relationship with genetics in the twentieth century and beyond. Graft hybrids offered many things: the possibility of fantastical new species, economically important new crops, and insight into alternate and unknown forms of heredity. Yet they repeatedly clashed with certain interpretations of genetics. By reconstructing their history, in this book I make three claims about twentieth-century heredity and biological experimentation. The first is that the very existence of graft hybrids challenged emerging techniques and concepts in genetics, shaping the discipline across the twentieth century. In this period, genetics was still a nascent science. Its grasp on biology and agriculture was not assured. Graft hybrids—living, breathing plants and animals beyond contemporary understanding—presented a real conundrum, or a real threat, to genetics. The years after the "rediscovery" of Mendelian genetics in 1900 have been described as a period "when hybridizers sought to fathom the limits and implications of Mendel's generalizations."[7] Graft hybridizers claimed not only to have discovered limits to Mendel's laws but also that graft hybridization could break these limits. After all, there were technically no obvious boundaries as to what organism could be grafted onto another.

The second argument I make in this book is that the twentieth-century decline of graft hybrids was gradual and overrated. Most scholarly attention to graft hybrids has been focused on two periods: the nineteenth century, a time when Charles Darwin found himself focused on plant grafting to understand heredity and development; and the appearance of the graft hybrid in the Lysenkoist biology of the Soviet Union from the 1930s onward. The intervening decades of the twentieth century, however, are equally fascinating. During this time the scientific discipline of heredity was gradually emerging, with no concrete consensus over its objectives or limitations. Furthermore, heredity was emerging against a "background of the formation of nation-states, with their centralized bureaucracies, capitalist economies, and imperialist aspirations."[8] Into this heady mix was thrown the graft hybrid. An intense debate over its true nature occurred just prior to the First World War. During the interwar years, several prominent supporters of graft hybridization could be found among European botanists and zoologists. The existence of graft hybrids was disputed, but by no means debunked. One important theme of this era was the failure of repeated attempts to bring experimentally produced graft hybrids into the scientific mainstream. These failures were often contingent or happenstance, with a series of lost specimens contributing to their mystery.

Third, and finally, I argue that graft hybrids were the most compelling part of Trofim Lysenko's biology in the Soviet Union. Defenders of Lysenkoism in the West, including the British biologists J. B. S. Haldane and Anne McLaren, pointed to graft hybrids when challenged to provide proof of Lysenko's doctrine. Unlike many aspects of Soviet biology, there was a genuine sense of the unknown surrounding graft hybrids. As I will show in this book, their existence was debated by scientists for much of the twentieth century, with no clear answers emerging. Thanks to this tradition, Lysenkoists' claims to have created graft hybrids were not unbelievable. In contrast to many of Lysenko's "experiments," graft hybridization was attempted by researchers across the Cold War world. Detailed accounts of graft hybrid plants and animals arose from Eastern Europe and China. Some of these experiments could not be replicated, while others left unexplainable results. Unfortunately for graft hybridizers, however, graft hybrids came to be rejected in genetics partly as a result of their association with Lysenkoism.

As Lysenko's attacks on genetics in the Soviet Union mounted, Western geneticists doubled down on the importance of classical genetics, dismissing Lysenkoism as pseudoscience. By the mid-twentieth century, any association with graft hybridization was to be avoided.

Graft hybrids were some of the strangest and most controversial beings that might never have existed. But before we can delve into their equally strange history, we must first explore the historical context in which these organisms arose to challenge narrow conceptions of heredity. The modern conception of graft hybrids developed in the late nineteenth century amid a sea of other hereditarian concepts and theories, including the biology of August Weismann and the rediscovery of Mendelian genetics at the dawn of the twentieth century. To understand some of the controversy surrounding graft hybridization, we must also investigate our current understanding of its role in the "Lysenko affair." In short, the twentieth-century history of graft hybrids touches upon some of the most important episodes in the history of biology.

The Graft Hybrid

Charles Darwin coined the term *graft hybrid* in his 1868 book, *The Variation of Animals and Plants under Domestication*, to describe an organism created through grafting that was identical to a typical sexual hybrid. It is possible, he wrote, that "two distinct species can unite by their cellular tissue. . . . Such plants, if really thus formed, might be called graft hybrids."[9] Darwin, however, had not come up with a new concept. He had simply named and defined an old idea in contemporary scientific language. Grafting was familiar to the ancient Greeks, although Aristotle struggled to fit grafted plants into his philosophical system, as they represented an awkward intersection between the artificial and the natural.[10] In the 1930s the classicist and amateur botanist Arthur Stanley Pease suggested that ancient writers, including the European "father of botany," Theophrastus, were wary of grafting between different species of plant lest they breach the "principle of limitation" that divided species. Pease, however, was reading the anxieties of his own time surrounding graft hybridization into classical texts.[11] Roman botanical texts and poetry had freely engaged with the "fantasy of unlimited transplantation."[12] By the nineteenth century, graft hybrids and their role in heredity became the subject of systematic inquiry by horticulturalists and botanists. Classical texts still made the odd appearance. In 1842 the editors of the *Gardeners' Chronicle*, a popular British horticultural magazine, were alerted to an outlandish claim in a rival publication. Someone had claimed to have produced a rare and valuable yellow rose by grafting a common red rose onto a broom (a type of flowering shrub). The *Gardeners' Chronicle* did not stand for such nonsense, suggesting that believers of such stories must have been reading too much Virgil or Columella, a sad indictment of the "nature of an English education."[13]

Early nineteenth-century commentators on what would soon be termed "graft hybrids" possessed a certain skepticism. Various accounts of such hybrid plants were gathered by Antoine Risso, former professor of physical and natural sciences at the Lycée de Nice, in partnership with Pierre-Antoine Poiteau, chief gardener of the Royal Nurseries of Versailles. Together they produced the monumental *Histoire naturelle des orangers*, published in 1818. In it, they refuted most claims that grafting could create new species. The Maltese orange tree, for example, was popularly claimed to be the product of a scion from an orange tree grafted onto a pomegranate shrub. Risso and Poiteau dismissed this account as an absurdity that had been disproved through experiment.[14] Yet one botanical puzzle eluded them. "Here is the most singular and curious tree of all the vegetable kingdom," they wrote of the Florentine Bizzaria. They accepted that the tree had likely been created by grafting but had no way of explaining its strange appearance. Other unexplainable botanical oddities also caught their attention. The duo located an orange tree in Nice that bore both bigarades and oranges and brought forth a mixture of red and white flowers.[15]

By 1868, Darwin was able to give two examples of famous graft hybrids that would have been familiar to his readers. One of them was the Florentine Bizzaria; the second was a tree known as the *Cytisus adami*, which Darwin described as a "form of hybrid intermediate between two very distinct species"; namely, the common and the purple laburnum.[16] The *Cytisus adami* had been created by Jean-Louis Adam, a Parisian nurseryman, before being brought to the attention of European botanists in 1830. One of the first on the scene was none other than Poiteau, who published several descriptions of the plant in the journal of the Parisian Society of Horticulture.[17] News of the unusual plant spread rapidly, with it winning several supporters. One British advocate was the clergyman and naturalist William Herbert, who claimed in 1840 that the existence of the *Cytisus adami* raised new and exciting possibilities. "If I am right in my notion," declared Herbert of his support, "it opens a field for the horticulturalist to produce hybrid plants which perhaps could not be obtained by seed."[18] Herbert's support demonstrates the appeal of graft hybridization to the practical plant breeder. If real, such organisms could bypass the natural limits faced by sexual crosses. In an ambition reminiscent of modern genetic engineering, almost any species could be combined with any other.

Darwin had begun his own investigation into the *Cytisus adami* in 1847, convinced that the tree could provide living evidence to support his belief "that the entire body of the organism had a role to play in determining heredity."[19] Although Darwin was not able to re-create the *Cytisus adami*, he nonetheless used *The Variation of Animals and Plants under Domestication* as a vehicle to introduce his own theory of heredity—pangenesis—to his Victorian peers. Put simply, pangenesis is the idea that each organ or cell of the body throws off a minute copy of itself. These copies, or "gemmules," then congregate in the sexual organs and are the means by which the physical characteristics of parents are passed on to their offspring.[20] If the units of heredity reside within the cells of living bodies, a graft hybrid would offer powerful evidence in favor of pangenesis. By taking the body part of one organism and surgically grafting it onto the body of another, the appearance of any characteristics resembling the grafted part in subsequent offspring would indicate that the wider body, not just the sex cells, could influence inheritance. Darwin was also able to present several accounts from gardeners and horticulturalists claiming that hybrid apples and roses could be made using grafting. Though compelling, however, these anecdotal stories were not enough. Darwin admitted that "it is at present impossible to arrive at any certain conclusion with respect to the origin of these remarkable trees."[21]

Shortly after the publication of *The Variation of Animals and Plants under Domestication* in 1868, Darwin received a letter from Friedrich Hermann Gustav Hildebrand, a German professor of botany at the University of Freiburg. Hildebrand had read Darwin's book and believed that graft hybridization could explain some strange results from his own experiments with potatoes. Hildebrand had grafted sprouts from white potatoes onto red potatoes, from which he managed to grow two bushes. Some of the potatoes brought forth by these bushes, he informed Darwin, "held the middle between the red and white potatoes: they were red and scaly at the one end, white and smooth at the other and in the middle smooth and white with red stripes."[22] This experiment convinced Hildebrand that graft hybrids did exist. However, his efforts to replicate his results had been unsuccessful. In another letter to Darwin, Hildebrand apologized for this failure. His two bushes had stopped producing potatoes and other attempts at grafting went nowhere.[23] Darwin directed his own gardener to graft differently colored potatoes together but did not come up with anything representing a hybrid.[24] Darwin and Hildebrand had run into a problem that would afflict research on graft hybrids for the next century: graft hybrids could not be reliably produced or replicated.

In the last quarter of the nineteenth century, an elderly and increasingly frail Darwin enlisted the aid of a young and enthusiastic naturalist to assist his search for a graft hybrid. George Romanes, like many other Victorian gentlemen of science, was engrossed by pangenesis. Romanes had been busy testing the theory by removing the ears of rabbits and other mammals for surgical grafting. Darwin encouraged him to abandon this approach and instead conduct grafting experiments on plants, particularly potatoes. From 1875 to 1880, Romanes grafted numerous species of plant together: potatoes, beets, onions, dahlias, peonies, and carrots. Regrettably, success was not forthcoming. Plants were lost to disease; grafted plants decayed or separated from their hosts. All the resulting seeds displayed the characteristics of only a single parent.[25] Results from other thinkers in the life sciences also spelled bad news for Darwin's theory of pangenesis. In 1871 the English polymath and eugenicist Francis Galton had found that transfusing blood from one variety of rabbit to another resulted in no "alteration of breed" in their offspring, demonstrating that "the doctrine of Pangenesis, pure and simple, as I have interpreted it, is incorrect."[26]

Galton was not the only skeptic. Charles McIntosh, a Scottish horticulturalist who had worked in the gardens of European monarchs and the British aristocracy, took a thoroughly practical approach to the question of graft hybrids. Drawing upon his extensive experience as a well-traveled gardener, McIntosh related several botanical observations that would cause the inquisitive mind to doubt tales of hybrids created by grafting. One could be seen by simply cutting into the point where two grafted plants were joined, at what was later referred to as the *graft junction*. McIntosh described how the two plants maintained their own distinctive "layers," which could be easily peeled apart from each other by hand. This indicated that grafted plants were mechanically pressed together, with no evidence of more fundamental intermixing or blending, an argument that would be formalized in the twentieth century via the formation of the chimera hypothesis. He also noted that many hundreds of trees were propagated through grafting at any one time. The vast majority of these plants maintained their distinctive identity and produced their own fruit.[27] If some kind of hybridization happened at all, it was rare.

These nineteenth-century interactions with graft hybrids display characteristics that would emerge time and again over the course of the twentieth century. Graft hybrids—and their existence or nonexistence—were bound up with fundamental questions about how heredity worked. In pursuit of answers to this mystery, little or no distinction was made between plant and animal graft hybrids. There were hints of the power that graft hybrids, in the form of new and previously unimaginable organisms, could grant their creators. Grafting could potentially burst through the species barrier, providing new plants and animals for agriculture that could not be obtained through other means. As for Darwin, he worked until the end of his life in an ultimately futile attempt to acquire a graft hybrid. If he had succeeded, then twentieth-century debates over the nature of heredity might well have been conducted on rather different grounds.

The Weismann Barrier

By arguing that hereditary material was produced throughout the body, Darwin's theory of pangenesis incorporated the age-old belief in the inheritance of acquired characters. The theory of acquired characters is most commonly associated with the French zoologist Jean-Baptiste Lamarck, who, in the early nineteenth century, proposed that parts of a living being could be gradually modified in response to changing environmental conditions, and that these modifications, which occurred during the lifetime of a single organism, could then be inherited by its offspring. His subsequent celebrity led to the emergence of "Lamarckians," a general epithet for those who stressed "the evolutionary role of individual variations that emerged during the life of an organism in response to environmental stress."[28] The most famous example given by Lamarck was the neck of the giraffe. By continually stretching its body to reach the scarce leaves on trees, went the theory, a giraffe had lengthened its neck and forelegs. These changes were inherited by its offspring, who repeated the process again and again across the generations until the giraffe had achieved its height.[29] For now, we can leave aside the question of what biological mechanism could explain this change and its inheritance. The key takeaway of this theory is that the body could adapt to changes in its environment, and that these changes could potentially be passed down on to its offspring.[30]

In the mid-nineteenth century, the inheritance of acquired characters was a relatively common idea, its presence arousing none of the ire directed at Lamarckism by modern biology. But scientific inquiries into the nature of the cell were already beginning to separate heredity from the development of the body during an individual's lifetime, thus undermining possible mechanisms by which alterations to the somatic (body) cells induced by environmental change could be inherited. In 1858 the German physician Rudolf Virchow theorized that there was "a division of labor" between the cell nucleus, which contains the chromosomes, and the cytoplasm, the liquid interior of the cell in which its organelles sit.[31] An elegant experimental demonstration of the importance of the nucleus in heredity was conducted by German zoologist Theodor Boveri in 1889. While based at the Zoological Station in Naples, Boveri removed the nuclei from the eggs of a genus of sea urchin. He then fertilized these eggs with sperm cells from another genus, which still contained their nuclei. The subsequent sea urchin larvae resembled only the latter. This result proved that it was the nuclei, not the cytoplasm, that shaped the developing larvae. The heredity process seemed to be confined to the nucleus of the cell. Boveri's experiment was well received, with the geneticist Thomas Hunt Morgan translating his report into English.[32] Morgan would later argue against Lamarckism and suggest that the chromosome was the site of the gene.

At the same time that Boveri was asserting the primacy of the nucleus, his countryman August Weismann was coming to a similar realization. Trained in medicine before turning to zoology, Weismann had once idolized Lamarck and Darwin. Yet in 1883 Weismann asserted that embryological "overgrowth" was a special phenomenon unique to the germ (or sex) cells. In 1885 he argued for the continuity of this "germ-plasm," stating that hereditary characters were passed down from parent to offspring through the germ cells alone. The somatic cells that make up the rest of the body had no role in this process. Since the germ cells of animals were distinct and isolated from changes in the somatic cells, this left no room for a mechanism by which the inheritance of acquired characters could occur. Weismann methodically rejected other heredity theories of his time, including Darwin's pangenesis, which suggested that acquired characters were transmitted from the body to the germ cells. Weismann's rebuff of acquired characters was "a deductive argument dependent upon the validity of his claim that a lineage of germ cells was significantly distinct from the soma."[33] This was the origin of what would later be referred to as the "Weismann barrier." The germ cells were partitioned from the somatic cells, passing hereditary material from generation to generation. Any environmental impact on the body, whether through injury or exertion, that did not affect the germ cells would not be passed on to the next generation.[34]

The establishment of the Weismann barrier did not mark the end of the Lamarckians. In 1888 Weismann had conducted a famous—albeit gruesome—experiment on mice. He cut off the tails of the mice and observed that this made no difference to their offspring; the next generation of mice possessed the same tails as their premutilated parents. If the Lamarckians were correct, argued Weismann, the tails of the mice should have eventually disappeared over the generations. The Lamarckians, ironically enough, adapted their claims to counter this evidence. Most now claimed that negative effects on the organism, including injuries, were not likely to be inherited by subsequent generations. They instead turned their attention to the inheritance of positive effects.[35] The acquisition of a new trait through grafting or transplantation counted as a positive effect. Although graft hybrids had been used by Darwin in his defense of pangenesis, however, they did not naturally fit into the Lamarckian framework. Acquired characters had generally been assumed to emerge through the use or disuse of an organ (as with Lamarck's example of the giraffe's neck) or as a direct response to a change in environmental conditions; for example, growing longer hair when placed in a colder climate.[36] Graft hybridization did not fall neatly into either of these categories. It was much more akin to traditional sexual hybridization, which Weismann and his supporters accepted. The only difference was that the hybridization event supposedly occurred via the somatic cells, not the sex cells. If this did occur, the Weismann barrier had been breached. Moreover, the very fact that the body could somehow be involved in heredity implied that the environment it was exposed to might also play a role in inheritance.

When it came to heredity, even the interior of the cell was a contested space. The Weismann barrier confined hereditary material not only to sex cells but specifically to their nuclei. Against this interpretation was the concept of cytoplasmic inheritance, which argues for the heritability of organelles in the cell (other than the nucleus). Cytologists—scientists who study cells—were one of several groups investigating how heredity worked in the early twentieth century. The field of cytology was closely related to embryology, with both disciplines examining how and why egg cells were able to develop complex organisms. Embryologists and their advocates, including the physiologist Jacques Loeb, attempted to take a more holistic view of inheritance and development, which involved speculating on "the existence of factors of heredity located in the cell cytoplasm."[37] Cytoplasmic inheritance pushed the Weismann barrier beyond the cell nucleus and chromosomes, but still restricted heredity to the sex cells.

Cytoplasmic inheritance provided an alternative to a strict interpretation of Weismann's theory well into the twentieth century. Its advocates included many European geneticists who experimented with plant hybridization.[38] In 1909 the German geneticist Erwin Baur showed that pigment-carrying plastids (the small organelles found in plant cells) were passed down through the maternal line of plants. Chloroplasts (where photosynthesis takes place) are a kind of plastid. Other kinds of plastids store energy or the pigments that give plants their color. Baur found that these plastids were inherited (just like the nucleus) across the generations, resulting in such phenomena as plants with distinct patches of green and white in their leaves.[39] Some German biologists used cytoplasmic inheritance to explicitly challenge the "nuclear monopoly" associated with American genetics.[40] Although cytoplasmic inheritance did provide an alternative to the most rigid interpretation of Weismann's results, its adherents were not necessarily open to even more radical forms of heredity like graft hybridization.

It is a sign of the complexity of heredity in the twentieth century that we find Baur acting as a steadfast opponent of graft hybrids and Lamarckism. He was also the originator of the modern chimera hypothesis, which debunked such splendid graft hybrids as the Florentine Bizzaria, and a critic of the Lamarckian Paul Kammerer, a Viennese zoologist who worked on graft hybrid salamanders. An interest in cytoplasmic inheritance did not necessarily lead to the embrace of graft hybridization (which went one step further than cytoplasmic inheritance by implying that somatic cells had a role in heredity). Graft hybrids, however, sometimes provided useful ammunition for those who wished to expand heredity beyond the confines of the Weismann barrier. The twentieth-century triumph of nuclear genetics over cytoplasmic inheritance was in part due to the inability to obtain experimental evidence of the latter and establish the "scientific techniques required to effect major change."[41] Even the briefest appearance of a graft hybrid threatened to reverse this imbalance, providing living proof that heredity was not confined to the sex cells.

With the rediscovery of Mendelian genetics in 1900, a new theory of heredity, free from the inheritance of acquired characters, presented itself for Weismann's scrutiny. At first Weismann was cautious. Experiments on gray and white mice at the laboratory of American geneticist William E. Castle seemed convincing. On the other hand, a 1901 report by two British Mendelians, William Bateson and Edith Rebecca Saunders, seemed to indicate to Weismann that the application of Mendelian genetics was not universal.[42] Initially, then, "for Weismann and the Weismannians Mendel's results seemed interesting but not central to the process of heredity." From this interpretation, Mendelian genetics only increased in importance after 1912, when chromosomes were established as the seat of heredity and reduction division in cells was better understood.[43] Nor were the later views of Weismann entirely clear, as he defended the idea that variation in the germplasm could have an external or developmental cause. This ambiguity "blurred the strong distinction [between heredity and development] that biologists, particularly geneticists, were forging." Weismann and the Weismann barrier were readily adopted by early twentieth-century geneticists in support of their science. However, some Lamarckians would also reinterpret Weismann to support their own views.[44]

Other ambiguities and seeming contradictions swirled around early twentieth-century heredity. In 1920 American botanist Albert Francis Blakeslee pointed out that mutations in plants were not confined to the sex cells. Genetically identical plants could therefore differ in their appearance from one another, thanks to changes in the number or organization of chromosomes in certain parts of their bodies.[45] Blakeslee distinguished chromosomal from genic mutations, attempting to induce the former using radium. His efforts, however, were overshadowed by the experimental success of the geneticist Hermann Joseph Muller, who focused on the role of the gene in heredity and induced mutations using X-rays.[46] In other national contexts, Mendelians and Lamarckians existed side by side. For a brief time, Mendelian genetics was praised by the Soviet Union for "establishing incontestably materialist laws of individual heredity." Yet genetics was believed to be incapable of explaining all facets of evolution, particularly the role of environmental change. Lamarckians, with their focus on the environment, were therefore also accepted. When Kammerer was accused of scientific fraud in the West, he was offered a laboratory in Russia by the Communist Academy's Section of Natural and Exact Sciences in 1925.[47] This period of tolerance came crashing down during the Lysenko affair. As we will see, a strong connection between Mendelian genetics and the Weismann barrier was not a logical necessity. It was, however, adopted by some geneticists to eliminate any hint of the inheritance of acquired characters and reinforce the exclusivity of their science. Heredity was an evolving area of scientific inquiry, the parameters of which had not yet been set.

Mendelian Genetics and Agriculture

During the mid-nineteenth century, a series of hybridization experiments on peas by an Augustinian friar threw up a series of intriguing results. Gregor Mendel's findings can be understood as a kind of algorithmic or mathematical system, which predicted what one should expect when crossing different plants.[48] Mendel began his experiments with garden peas, which have simple inherited traits, easily tracked across the generations. The peas are, for example, either yellow or green, smooth or wrinkled. If you crossed a plant with green and round (gR) peas with another with yellow and wrinkled (Yw) peas, you might end up with a new hybrid bearing yellow and round (YR) peas. In this case, the yellow and round (YR) characters were what Mendel defined as "dominant" factors, while the green and wrinkled (gw)—which did not appear in this first generation—were "recessive," hidden away within. Mendel did not stop there. He then allowed his hybrid pea plants, which in this case were always yellow and round (YR), to self-pollinate. Instead of simply producing more of the same, the offspring of these plants possessed a mix of characters. Some of their peas were yellow and round (YR), some yellow and wrinkled (Yw), some green and round (gR), and the odd one was even green and wrinkled (gw). Mendel had found that both dominant and recessive characters were passed down the generations, with the former masking the latter in the first generation. The combination and recombination of pea plants led to some of the recessive characters emerging in a predictable ratio. With a single character in play, this ratio was approximately three to one in favor of the dominant character. In our example, with two characters in play, the ratio in the second generation was nine to three to three to one (with the dominant yellow and round (YR) again more numerous).[49]

That is Mendel and his insight. By carefully selecting and breeding simple organisms, the Augustinian friar had been able to remove "the baffling clutter, the signal-muffling noise that defeated previous investigators" from the mysteries of heredity.[50] Extracting predictable ratios from the heritable traits of cross-bred pea plants was not only of theoretical interest. Mendel's abbey at Brno, in the modern-day Czech Republic, was not some hermetic retreat. Producing new and stable hybrids was of great interest to farmers in the region, which was particularly famous for its sheep. Mendel's abbot had been active in the world of sheep breeding, while Mendel himself had been trained in horticulture and was a member of the Natural Science Section of the Agricultural Society in Brno.[51] Despite his connections to agricultural interests and other plant hybridizers in Europe, however, Mendel's discoveries famously failed to produce much in the way of scientific or economic impact in his lifetime. In 1900 three academic biologists with interests in plant breeding—Hugo de Vries, Carl Correns, and Erich von Tschermak—independently rediscovered Mendel's laws. The Augustinian friar was subsequently declared the founder of genetics. However, the near-simultaneous claims of uncovering Mendel served the individual interests of the scientists involved, rather than pointing to some historical inevitability that Mendel would eventually be proved right.[52] Key principles in genetics were developed only after the 1900 rediscovery, while de Vries ended up sidelining Mendelian genetics in favor of his own theory of heredity.[53] Regardless of the specific circumstances of who discovered what and when, by the early years of the twentieth century Mendel had followers in the scientific community, some of whom made grandiose claims that the friar's system would revolutionize agriculture.

The extent to which Mendelian genetics could be applied to early twentieth-century agriculture is also controversial.[54] Appeals to the mathematical elegance of Mendel's work likely carried little weight with farmers who, as we will see, were much more interested in practical results than in theoretical explanations. There were good reasons, however, why Mendel's system might be embraced by some. In the United States, the new science of genetics fit with a preexisting trend toward the rationalization of agriculture and an influx of new capital into that sector.[55] The emergence of "genetic rationality," or the bookkeeping involved in recording and organizing data on Mendelian crosses, reflected an emphasis on systematic and rational administration already embraced by industries as diverse as transport and consumer research.[56] Another aspect of Mendel's work that appealed to capitalist thinking was that economically useful traits in plants and animals existed as discrete entities that could be carried between organisms through hybridization and passed down onto future generations. This raised the possibility that living things could be subject to the same intellectual property laws that governed machines and other forms of technology. A 1906 bill placed before the US Congress, for instance, argued that seeds could be patented, as they were mechanisms in the same way a trolley car was.[57] Outside of the United States, growing demands for food and raw materials from urban populations and industry led to the foundation of academic institutions and agricultural stations devoted to plant breeding. Leading facilities were established in Scandinavia, Germany, and Russia by the early twentieth century, at the very moment that Mendelian genetics came into being.[58]

Mendelian-style breeding was not universally welcomed by farmers, however. Sexual hybridization of crop plants, particularly on a large scale, was time-consuming and costly. Control of plant breeding and seeds therefore moved away from farmers and into the hands of private enterprise.[59] Genetics faced a turbulent reception in different national contexts. In France, the "alleged predictability" of Mendelism fell apart when faced with the reality of cereal breeding in the 1900s.[60] A similar problem arose in Britain, where the famed plant breeder Rowland Biffen struggled to apply Mendelian principles to breeding disease-resistant wheat.[61] The worlds of breeding and agriculture were hotly contested spaces, with their inhabitants able to choose from an array of techniques and theories to suit their needs. One of the better-known options was de Vries's mutation theory. In 1901, de Vries, one of the three rediscoverers of Mendel, used the plant *Oenothera lamarckiana* (now *Oenothera glazioviana*) to argue that mutation allowed evolution to occur in sudden leaps and bounds, not slowly and gradually as argued by Darwinians. De Vries visited the United States in 1904, where his mutation theory raised hopes that a shortcut to breeding new types of plants and animals had been found, quelling fears of a growing population outstripping food supply.[62] Unfortunately, de Vries had chosen a plant with highly complex genetics that gave out the false impression of rapid evolution. Excitement over the economic applications of his theory was short-lived, with its popularity beginning to wane by the outbreak of the First World War.[63] As we will explore, the graft hybrid represented another contender for agricultural improvement.

The science of genetics did not stand still across the twentieth century. New findings altered the discipline and informed its adherents' attitudes to graft hybridization. One of these findings came about through the interaction of an American geneticist, Thomas Hunt Morgan, with a new model organism: the fruit fly (*Drosophila melanogaster*). The fly had many advantages for laboratory study. It had a simple genome, was easy to breed, and had a short lifespan, thereby cutting down on the time and cost usually involved in genetic research.[64] Morgan and his students observed the Mendelian system at work in fruit flies and went on to theorize that the chromosome was the seat of heredity. Beginning in 1910, they found that certain characters—such as eye color—were linked to patterns of sex chromosome inheritance in flies. When Morgan teamed up with Frans Alfons Janssens, a Belgian cytologist, they hypothesized that Mendelian characters were carried along the chromosomes, crossing between them during cell division with a frequency relative to their position. Morgan used these insights to argue that genes were the units underpinning heredity. He and his supporters subsequently "deemphasized hereditary phenomena that could not be explained by their theory."[65] This assertion caused some embryologists to protest "the exclusive role of the nuclear gene in heredity," arguing that Mendelian genetics accounted for only relatively trivial characteristics within a species. The cytoplasm, they claimed, played a more important role in fundamental evolutionary change.[66]

Another important aspect of twentieth-century genetics was eugenics, the troubled application of heredity principles to humanity. Many of those involved in the various controversies over the existence of graft hybrids were enthusiastic eugenicists, including Bateson, Baur, Castle, and their fellow geneticist Charles Davenport. Some graft hybridizers were also eugenicists. Kammerer advocated a kind of Lamarckian eugenics, arguing that environment and education could heal and improve humanity.[67] The actual incorporation of eugenics into scientific discussions of graft hybridization was rare, but not unheard of. An exchange in the American *Journal of Heredity* in 1927 included a contribution by the geneticist Robert C. Cook, who argued that references to cross-species grafting in the plays of Shakespeare indicated that they were actually authored by the natural philosopher Francis Bacon. Cook suggested that it would be near-miraculous if "the random Stratford boy, abandoning his wife and children at twenty" could have produced such masterpieces. Under the eugenic framework, genius and scientific knowledge were more likely to be the hallmarks of a morally upstanding member of society from an esteemed family. "The authorship of the plays by a person with Bacon's breadth of interest and literary endowments," argued Cook, "is much more explicable biologically."[68] Overall, however, graft hybrids were of more interest for their apparent ability to breach both the Weismann barrier and the barriers between species. The conflict between geneticists and graft hybridizers would later take on a political flavor with the outbreak of the Cold War.

Grafting in the Cold War

One of the darker episodes in the history of science took place in the Soviet Union with the rise of Trofim Lysenko, a peasant-farmer-turned-agronomist. His career had begun amid the 1927 collectivization campaign in the Soviet Union, when Joseph Stalin persecuted those deemed "kulaks" (wealthy peasants) and instigated a famine in Ukraine. Soviet propaganda of this period depicted Lysenko as a "barefoot scientist" whose practical, almost rustic, skills had earned the gratitude of the people and the praise of agronomic experts.[69] By 1933, Lysenko had taken control of the Institute of Plant Breeding and Genetics in Odessa, despite a lack of any formal scientific training. Here he promoted vernalization—a technique involving the exposure of growing seeds to cold in order to speed up their progression to the point of flowering—of major crops such as wheat and cotton. Plant physiologists in the Soviet Union cautiously accepted some aspects of Lysenko's work, which found a more welcome reception among the Communist Party bureaucracy. Vernalization, however, did not live up to Lysenko's promise and was quietly dropped.[70] Lysenko's early forays into heredity and genetics had been roundly criticized by both plant breeders and academic biologists. By 1935, Lysenko's political standing had raced ahead of his achievements. He was lauded by newspapers, supported by Stalin, and a member of the prestigious V. I. Lenin All-Union Academy of Agricultural Sciences, becoming its director in 1938.

Lysenko's final triumph over the entirety of Soviet biology came in an infamous meeting of the Academy of Agricultural Sciences in 1948. Lysenko denounced classical genetics, claiming that Weismannism and Mendelism-Morganism (the latter term referring to the idea that chromosomes contain heredity information) had "been primarily directed against the materialist foundations of Darwin's theory of evolution."[71] In short, he was throwing away the whole of genetics and chromosome theory as a harmful bourgeois science, antithetical to the values of the Soviet Union. Protesting this attack would have been unwise. By the time of the 1948 meeting, Lysenko's primary opponents were dead or had been forced aside. The botanist and agronomist Nikolai Vavilov, the former director of the Academy of Agricultural Sciences, had died in prison in 1943.[72] Muller, an American, had fled the Soviet Union some years earlier. In a misguided attempt to win Stalin over to the geneticist camp, Muller had sent the Russian dictator a copy of his book, *Out of the Night*, which promoted eugenics. Stalin was displeased and Muller fled.[73] In case there was any doubt as to where the dictator's sympathies lay, Stalin carefully proofread and edited Lysenko's 1948 address.[74] With such powerful political backing, Lysenko was able to lay out his vision for biology, which included a form of Lamarckism and an emphasis on cooperation between organisms, without much in the way of evidence that any of his ideas worked.

Here is where the graft hybrid came in. Graft hybridization had maintained a respectable presence in biology well into the 1930s. This history meant that Lysenko's claim that new plants could be produced using grafting was one of his few ideas with any credibility beyond the Soviet Union. In 1945, Lysenko displayed some tomato graft hybrids at a lecture to mark the 220th anniversary of the Russian Academy of Sciences. Julian Huxley, evolutionary biologist and science writer, was in attendance. A British colleague suggested that fraud was afoot, with the plants displayed by Lysenko probably obtained from existing varieties, not by grafting. Huxley also noticed that the tomatoes displayed at the lecture were wax models.[75] At his 1948 address to the Academy of Agricultural Sciences, Lysenko displayed more graft hybrids. He declared that their existence breached the Weismann barrier and lay beyond the explanatory power of classical genetics. He was not, however, open to discussing how or why graft hybridization occurred. In 1949, Jean Brachet, a Belgian embryologist and member of Belgium's Communist Party, visited Lysenko. Brachet suggested that graft hybrids might be the result of "self-replicating virus-like genetic particles in the cytoplasm" of plants, which could reach out and invade the rest of the body. He proposed an experiment to reveal whether this was the case, suggesting that a membrane be inserted between two grafted plants that would block the passage of these hypothetical particles. Lysenko had no interest in experiments conducted only for scientific curiosity, which he regarded as a symptom of capitalist excess. Brachet returned home and denounced Lysenkoism.[76]

Clearly, then, Lysenko did not draw upon the experimentally minded graft hybridizers of Western Europe and North America for inspiration. His vision for biology may have been informed by a much older tradition, with its roots in the nineteenth-century acclimatization movement. Acclimatization—the theory that plants and animals could adapt to new environments over time—was embraced by prominent Russian thinkers associated with the "Westernization movement" of the 1840s. The ambition to control the evolution of species through the environment, expressed by bodies such as the Moscow Agricultural Society and the Imperial Russian Society for the Acclimatization of Animals and Plants, would become an integral part of Lysenkoism.[77] Neo-Lamarckism was also prevalent in the Russian life sciences. Ivan Pavlov, famed for his behavioral experiments with dogs, was a believer in the inheritance of acquired characters and suggested that even behavioral reflexes (such as dogs salivating at the sound of dinner bells) could be ingrained in the organism over generations.[78] Kammerer, a Lamarckian, was idolized as a hero in the early Soviet Union. The 1928 Soviet-German movie *Salamandra*, which was produced after claims of scientific fraud and

Kammerer's suicide, depicts Kammerer as the victim of a conspiracy who is eventually saved by the Soviet Union.[79]

Lysenko claimed that one of his most important influences was Ivan Vladimirovich Michurin, a Russian horticulturalist. During the early years of the twentieth century, Michurin had achieved a level of fame as a self-taught plant breeder, producing hybrid fruit trees that could replace imported varieties. He also believed in the existence of graft hybrids, coming up with his own "mentor" method of producing them. This involved grafting young shoots onto old stock, in the belief that the more mature plant would exert a greater influence over the developing scions. In later life, Michurin was lionized by the Soviet state, which portrayed him as a patriotic hero fending off offers from American capitalists to buy out his research.[80] Lysenko would adopt Michurin's beliefs regarding graft hybridization wholesale. Michurin, however, never denied the reality or applicability of Mendelian genetics. We will see how Western commentators realized that Michurin had been misrepresented by Lysenko, and explore how "Michurinism" became both a substitute term for Lysenkoism in the Soviet Union and a label with which one could express support for graft hybridization in the West without mentioning Lysenko. As for Lysenko's biology, we are forced to agree that "where he was right, he was not original; where he was original, he was not right."[81]

The Lysenko affair, as the Soviet attack on genetics is sometimes called, had global repercussions. Renewed contact with Soviet scientists after the Second World War gave their Western colleagues the impression that Lysenko's position was not unassailable. Geneticists in Britain and the United States organized anti-Lysenko campaigns. Among their number were the exiled Muller and Huxley, who had seen Lysenko's wax models of graft hybrids firsthand. The outbreak of the Cold War, however, would cause these international links to become a liability to Soviet geneticists.[82] When Lysenko asserted his scientific and political dominance in his 1948 lecture, Lysenkoism began to be labeled as "pseudoscience" in the United States.[83] One casualty of the growing Cold War divide in biology was research into chromosomal mutations. In 1927, Muller had bombarded the sperm of *Drosophila* fruit flies with X-rays, creating alterations to their chromosomes that could be passed down through three or four generations.[84] In the United States this result was taken as the result of genetic mutations. In the Soviet Union it was interpreted as an example of the influence of the environment on inheritance.[85] Lysenko was not inclined to alter the organism through chemicals or radiation. Although he did not deny the effects of such methods, he viewed them as a kind of "poison" that "can only rarely and only fortuitously lead to results useful for agriculture."[86] During the 1940s and 1950s American biologists also downplayed the importance of chromosomal mutations. Heredity was simplified to the level of the gene, while the mere fact that Soviet biologists had shown an interest in chromosomal mutations was enough to dissuade their American counterparts from following suit. Now, "heredity in the West was increasingly defined, refined, and constrained in opposition to Lysenkoist interpretations."[87]

In other national contexts, a visceral rejection of all things Lysenko did not occur. One example is that of postwar Japanese genetics. When information on Lysenko's experiments was circulated among Japanese geneticists during the 1940s and 1950s, some were intrigued by Lysenko's graft hybrids. Hitoshi Kihara, an internationally prominent expert in wheat genetics at Kyoto University, even "suggested some alternative possibilities to interpret the graft hybrid from the viewpoint of orthodox genetics," a stance that was also adopted by British biologists with sympathies for Soviet biology.[88] Kihara was far more critical of other aspects of Lysenkoism. In 1953 he and geneticist Karl Sax coauthored an article in which they mocked the Lysenkoist claim to have transformed wheat into oats or rye by planting it in different environments. "By inference," they wrote, "we might assume that under suitable conditions, perhaps by proper housing or diet, the Soviet scientist will be able to convert Orang-outangs into humans or vice versa."[89] Unlike their American counterparts, Japanese geneticists made space for the role of the cytoplasm in heredity. The appearance of the inheritance of acquired characters in Lysenkoism did not unduly worry Japanese researchers either. Kihara noted that when some bacteriologists in Japan called themselves Lysenkoists, they only meant that they worked on adaptive mutations or the inheritance of acquired characters.[90]

In addition to the denouncement of Lysenko, the Cold War also saw the crowning of Mendel as the "father of genetics." In 1950 the Genetics Society of America celebrated the fiftieth anniversary of the rediscovery of Mendel, generating widespread radio and newspaper coverage. The society had held back from speaking out against Lysenkoism, but now found the perfect opportunity to use the celebrations "to present a positive, dignified, and powerful alternative."[91] Many of the participants in a scientific panel assembled by the society, including Huxley, were aware that the general public could become lost amid the subtle distinctions between neo-Lamarckism, cytoplasmic inheritance, and gene expression. Their solution was to present

Mendel as the common ancestor for all the varied forms of modern genetics. Not every biologist was willing to accept this elevation of Mendelism. The geneticist and future Nobel Prize winner Barbara McClintock stayed away on the grounds that the Genetics Society's anniversary event was "a celebration of the triumph of classical genetics."[92] This period also saw the association of Mendelian genetics with the development of hybrid maize in the United States. During the Cold War, this event would be promoted as a triumph of Western plant breeding over the agricultural failures of Lysenkoism.[93]

The Cold War did strange things to the graft hybrid. Graft hybridization maintained a small, yet respectable, following in Western biology into the 1930s. The rise of Lysenko shook up this cozy situation. The Cold War thrust the graft hybrid back into the scientific spotlight and subjected it to fresh scrutiny, decades after some of the most intense exchanges over their existence had passed. Unfortunately for defenders of the concept, graft hybridization was now associated with all the unpleasantness of Lysenko and the Stalinist regime. As we will explore, some defenders of Soviet science, notably Haldane, halfheartedly pointed to graft hybridization as evidence that Lysenko's theories had some validity. McLaren turned this approach on its head, using the relative strength of graft hybrids as a scientific concept to promote her version of Marxist biology. The Cold War division of biology had a lasting impact. We will see how practitioners of cell fusion were wary of comparisons to graft hybridization. Although the two techniques had their similarities, the graft hybrid had become a tainted idea. The twentieth century would pass before its existence was again debated in Western science.

Structure and Concluding Remarks

Before we begin our journey into the world of the graft hybrid, a few words of caution. Heredity in the twentieth century is a complex affair. Each of the actors we encounter in this book was a complicated character, and many of them held what we would today consider ambiguous or contradictory beliefs. William Bateson, the British Mendelian who attempted to interpret the development of graft hybrids, did not believe in chromosome theory.[94] His colleague the German geneticist Erwin Baur attacked various graft hybridizers over the course of his long career in biology. Baur, who pursued research on mutation and recognized the complex relationship between Mendelian genetics and the environment, was no ordinary Mendelian. His full-throated defense of the field was directed "against those who tried to limit Mendelian validity," such as the graft hybridizers.[95] The graft hybridizers themselves had complex beliefs that did not necessarily clash with genetics. Charles Claude Guthrie thought that his graft hybrid chickens might simply represent an extra hereditary mechanism. Paul Kammerer and Ivan Vladimirovich Michurin, both graft hybridizers, also accepted the validity of Mendelian genetics. A similar level of complexity haunts our efforts to define what a graft hybrid was at any given time. I have attempted to stick with the spirit of Darwin's definition when referring to "graft hybrids," as it was usually the case that a plant or animal hybrid created through grafting or transplantation was called a graft hybrid. Nevertheless, there were exceptions to this rule.[96]

This book consists of six chapters, ordered chronologically, which trace the graft hybrid throughout the twentieth century and its revival in the twenty-first. These chapters do not constitute an exhaustive account of every twentieth-century graft hybridizer, but do focus on important debates, collaborations, and exchanges between notable players in the field.[97] Chapter 1, "A Poultry Affair," jumps straight into an early twentieth-century graft hybrid controversy, examining the uptake of Mendelian genetics in the United States, and how and why Guthrie, an American physiologist, came to believe that he had created graft hybrid chickens. A series of indecisive back-and-forth experiments between Guthrie and the geneticist William E. Castle sets the scene for the debate between graft hybridizers and geneticists for the rest of the century. In chapter 2, "Rise of the Chimera," I consider what was defined as a graft hybrid in more detail, focusing on the scientific reception of a tomato-nightshade hybrid created by the German botanist Hans Winkler. In chapter 3 I explore how scientific belief in graft hybridization persisted into the interwar period, following the graft hybrid salamanders of Paul Kammerer and efforts by the British botanists Frederick Ernest Weiss and William Neilson Jones to locate graft hybrids and account for their origins.

After the Second World War and Lysenko's attacks on geneticists in the Soviet Union, the graft hybrid became entangled in the wider ideological clash of the Cold War. In chapter 4 I explore this tension through a series of encounters between British scientists and plant breeders with their counterparts in the Soviet Bloc. In chapter 5 we encounter the British zoologist Anne McLaren, whose politics and frustration with the limits of Mendelian genetics led her on a global search for graft hybrids. Over the course of her career, McLaren would encounter graft hybrid poultry in Hungary, tomatoes in Yugoslavia, eggplants in China, and peppers in Japan. In chapter 6 I describe the relationship between graft hybridization and the field of somatic hybridization (a form of cell fusion) in the mid-to-late twentieth century. Unlike the graft hybrid, cell fusion was once celebrated in the West as the future of biotechnology. Its practitioners attempted to distance themselves and their science from the ideologically charged (but closely related) technique of graft hybridization. I conclude with the contemporary revival of the graft hybrid in the twenty-first century. Although its connotations with Lysenkoism remain problematic, grafting is recognized as a means by which one plant can transfer genes to another. Despite a century of controversy, the graft hybrid has now been incorporated into modern biotechnology.

Before we launch into the history of the graft hybrid, there is one final matter to clear up. What was the true nature of the famous Florentine Bizzaria we encountered at the start of this chapter? Shortly before the outbreak of the First World War, some botanists theorized that plants like the Bizzaria were not true hybrids. They were instead chimeras, two genetically distinct organisms intertwined in a single body.[98] Though named after the fire-breathing monster of Greek mythology, real-world chimeras are quite common. A mutation in the pink flowers of a peach tree, for example, can give rise to genetically altered cells, leaving white patches or flecks in the flower where the new cells have grown.[99] Chimerism can also happen to humans. Cellular traces of a fetus can persist in the body of the mother for years after pregnancy, or two zygotes can occasionally fuse together. More commonly, cells with a different genetic code are introduced to our bodies via medical interventions, such as in organ and bone marrow transplants.[100] The Florentine Bizzaria, however, was more dramatic in its appearance than these examples. Not only was it composed of different species but its cellular tissues of citron and orange were seemingly inseparably mingled.

During the winter of 1922 to 1923, Tyôzaburô Tanaka, a member of the Phytotechnical Institute at the Miyazaki College of Agriculture in Japan, traveled to Italy. Tanaka visited the Botanical Institute of the University of Florence and then the Giardino Botanici Hanbury of La Mortola, where he found a specimen of the Bizzaria. When he examined the plant, he found that it consisted of a citron core surrounded by an external skin of sour orange. Tanaka theorized that the Bizzaria was the result of different elements battling for space in the body of a single plant. He could explain the appearance of the plant using the chimera hypothesis, without reference to hybridization. “Critical study of this much discussed graft-hybrid,” concluded Tanaka, "thus brings us to the conclusion that this is a clear case of periclinal chimera."[101] A periclinal chimera refers to a type of chimera in which the genetically different cells occupy different layers of tissue—in the case of the Bizzaria, leading to a plant that is largely citron, but with a skin (or bark, in this case) made of cells from an orange tree. Despite its fantastical appearance, then, the Bizzaria was far from the most intriguing or compelling example of a graft hybrid. It is to these organisms we now turn.