From: J. Endersby, A Guinea Pig's History of Biology (HUP: Cambridge, 2007)

Chapter 6

Drosophila melanogaster: Bananas, bottles and Bolsheviks

Like most children, my son's favourite fruit is the banana, which gives him something in common with Darwin, who also loved them. In 1876, when Joseph Hooker (by then director of Kew) sent his sweet-toothed friend bananas from Kew's hothouses, a delighted Darwin responded that 'You have not only rejoiced my soul, but my stomach, for the bananas are simply delicious. I never saw any like them.'[1] Bananas were then a rare treat, even for the comparatively wealthy Darwin – most Victorians would never have even seen one. Many Americans tasted their first banana in the same year, at the Philadelphia Centennial Exposition, where they could have bought a single banana, carefully wrapped in tinfoil, for 10¢. Despite the cost (over $10 in today's money), the bananas were so popular with visitors that guards had to be posted to prevent visitors pulling the trees apart for souvenirs.

Inspired by their popularity, an American ship's captain, Lorenzo Dow Baker, bought 160 bunches of bananas in Jamaica and freighted them to Jersey City in the US, where he sold them for a 700 per cent profit. Inspired by this success, he teamed up with a Bostonian merchant, Andrew Preston, determined to develop the banana market; the long-term result of their efforts was to be the United Fruit Company (now Chiquita).

It is unlikely to be a coincidence that in 1875, when bananas

were starting to become common on the east coast of the United States, another exotic foreigner was first spotted in New York, a species of fruit fly which bug-hunting naturalists identified as *Drosophila ampelophila*. The name *ampelophila* means 'lover of grapes', reflecting its close association with fruit, especially with wine, but the species is now known as *melanogaster*, which – rather less glamorously – simply means 'black-bellied'. No one knows how this species arrived in New York, but the timing suggests they came in with shipments of fruit, probably from central America and the Caribbean, where most of the USA's tropical fruit still comes from.

Drosophila and bananas go together. As Groucho Marx once observed, 'Time flies like an arrow; fruit flies like a banana.' Together, flies and bananas created modern genetics by developing Mendel's vague *Anlagen* into genes, but they could not have done so (nor would bananas have become part of either my son's diet or Darwin's) without slavery, the impact of colonialism and a rather curious genetic behaviour called polyploidy.

As humans have moved across the globe, we have carried seeds with us, spreading our crop plants all over the world, so it is now difficult to know exactly where and when the wild ancestors of many of our domesticated plants evolved. Bananas are no exception – we have been eating them since before we could write, so there are no records of when and where we first found them. However, we can get a pretty clear idea by looking at where their wild relatives grow today. Modern commercially grown bananas are derived from two species of the genus *Musa* that are widespread across south-east Asia as far as India. By studying the overlap of the wild species, botanists have concluded that they almost certainly originated in what is now Malaysia. A similar exercise for Drosophila reveals a similar pattern: they too almost certainly evolved in the jungles of south-east Asia, so it is more than likely that as bananas and other tropical fruits were spread around the world by humans, the flies came along with them.

Most scholars credit the Arabs with bringing bananas to the Middle East and thence to Europe. They are considered a holy

plant in the Koran – indeed both Islamic and some early Christian scholars considered them to be the first fruit that humans ate; there is even a Christian tradition that identifies bananas as the 'forbidden fruit' in the garden of Eden, a story which inspired Linnaeus to name one species *Musa paradisiaca.* Bananas were spread throughout sub-Saharan Africa by Arabic traders; western explorers reported them growing there in the late fifteenth century. Evidence of the Arabic influence comes in the name itself: 'banana' derives from West African names for the fruit, which were in turn derived from the Arabic *banan*, or 'finger'.

Bananas reached the Caribbean in 1516, thanks to Friar Tomás de Berlanga, a Catholic missionary of the Dominican order of Predicadores (preachers), who is best known for discovering the Galápagos islands. He brought African bananas to the island of Hispaniola (the present-day Dominican Republic and Haiti), where they were intended as a cheap food for the island's growing population of African slaves. When Berlanga became bishop of Panama he probably took bananas with him to the mainland, where they spread so rapidly that many later travellers assumed they were indigenous to central America.

Drosophila probably reached the Americas at about the same time as the banana, but the flies had been known to Europeans much earlier. They are first mentioned in Aristotle's *Historia animalium* ('History of Animals'), where he describes an insect whose grub 'is engendered in the slime of vinegar'.[2] Aristotle referred to this insect as 'conops', which translates as gnat or mosquito. ('Conops' is the source of the English word 'canopy', from *conopeum*, which originally meant a bed with a mosquito net.) The various references to conops in Aristotle seem to conflate several different insects, since he says some draw blood while others will only eat sour things, like vinegar, not sweet things. So Aristotle perhaps confused mosquitoes with vinegar flies (one of the common names for Drosophila).[3]

It might seem unlikely, given how different bananas and vinegar are, that they are eaten by the same insect, but Drosophila

are in fact not fruit flies at all; they are not even closely related to the real fruit flies, which devastate fruit crops. Drosophila live on yeasts, the products of fermentation and decay. It is not fresh bananas but over-ripe and rotting ones that attract the flies; as they go bad, they ferment – producing yeasts for the flies to feed on. Anywhere that fruit is going bad, there are Drosophila.

Of course, humans do not only ferment fruit by accident. As *Drosophila melanogaster*'s original name, *ampelophila,* records, humans like to ferment fruit to produce alcoholic drinks. (Another name for them, common in the early twentieth century, was pomace fly – pomace being the mashed apple that is left after cider-making.) Shipments of rum probably had as much to do with Drosophila's arrival in the United States from the Caribbean as did shipments of fresh fruit. In the early nineteenth century, two English naturalists, William Kirby and William Spence, named these insects Oinopota, which means 'wine-drinker', christening one species *Oinopota cellaris*, because they believed it was only found in cellars where wine and beer were stored.[4] *Oinopota cellaris* found a place in one of the most remarkable books of the nineteenth century, the best-selling *Vestiges of the Natural History of Creation* (1844). Its anonymous author used the existence of this fly which 'lives nowhere but in wine and beer, all of these being articles manufactured by man' as evidence of the spontaneous generation of life.[5] The author, now known to have been the Edinburgh publisher Robert Chambers, reasoned that the flies could not have existed before humans were helpfully stocking cellars for them. And since they could not survive outside the cellars, they must have arisen, *in situ,* over and over again; whenever and wherever the right conditions existed, the flies were spontaneously generated.[6] (Obviously the flies were not spontaneously generated in cellars, any more than they are in your fruit bowl; their eggs are simply too small to be visible to the naked eye.)

Despite their cellar-dwelling and obvious fondness for alcohol, the name Oinopota did not stick. Although they evolved in the tropics, these insects cannot cope with too much heat – as the temperature rises, they become sterile and eventually die. So,

unlike mad dogs and Englishmen, the flies avoid the midday sun; they are usually active around dawn and dusk, which is why in 1823 the Swedish naturalist Carl Frederik Fallén renamed them Drosophila, which literally means 'dew lover'.

Thanks to the enterprising efforts of Catholic missionaries, slave traders and the United Fruit Company, bananas – and fruit flies – became increasingly common in American cities towards the end of the nineteenth century. By the first decade of the twentieth century, United Fruit effectively ruled the Caribbean 'banana republics' it dealt with, owning everything from the plantations, the ships and railroad cars, to the markets where the fruit was sold. They had the growing and shipping of bananas so well organized that they were able to supply them all year round, right across the United States. By 1905, the company imported forty bananas a year for every man, woman and child in the USA; by 1920, it had become one of America's largest corporations. A combination of steamships, railroads, refrigeration and ruthless business tactics turned the banana from a luxury item into America's most popular fruit.

Race, class and fruit flies

The speed with which bananas – and flies – could travel from Jamaican plantations to New York kitchens was just one symptom of the pace of the twentieth century. New technologies such as refrigerated transport made it possible for people to eat new things, but the growing prosperity of the United States by the early twentieth century was also crucial in creating the demand for exotic technologies and foods. In the late 1890s, appalling harvests in Europe had coincided with bumper ones in America; as exports soared, American factories and farmers found they could not keep pace with demand across the Atlantic. Unemployment fell so fast that a labour shortage seemed possible and American producers worried that their domestic market was becoming saturated. Immigration was the solution to both problems, and millions of Europeans poured across the Atlantic, escaping pogroms and hunger, hoping for freedom and

prosperity. A second great migration brought hundreds of thousands of African-Americans from the south to the north, leaving behind lynch mobs and plantations for work in the seemingly ever-growing factories. The USA was transformed.

The millionaire Andrew Carnegie marked the new century with a new edition of his book *The Gospel of Wealth*. The title brashly expressed the self-confidence of US industry that having put millions to work – and put bananas on every table – American business savvy held the key to solving the world's problems. If everywhere could be like the USA, everyone could be clothed, housed and fed. Carnegie backed his judgement by investing millions in ambitious philanthropic schemes, such as the Carnegie Institution of Washington, which – as we have seen – invested heavily in biological research, intent upon vanquishing disease and hunger. Like most of his contemporaries, Carnegie assumed that competition was the key to progress: 'It is to [the law of competition] that we owe our wonderful material development, which brings improved conditions in its train.' He argued that competition was 'not only beneficial, but essential to the future progress of the race'.[7] Carnegie's contemporaries also saw competition as a law of nature, as Darwinism in action; as one of them wrote, 'millionaires are a product of natural selection'.[8]

Darwin had borrowed his metaphor of natural selection from industrial capitalism; believing, like most Victorian gentlemen, that competition between rival businesses led to the best products dominating the market, he reasoned that similar competition between organisms would lead to the best-adapted dominating the reproductive market – by producing the most offspring. So, using Darwinism to prove that capitalism was natural was perhaps rather a circular argument, but men like Carnegie were not daunted by such considerations. They rather tended to worry that there might not be enough competition to ensure continued progress. As prosperous nations like the United States got even wealthier and technology made life easier (at least for some), Carnegie and others were concerned that the sharp edge of natural selection was being blunted and that instead of

progressing, Americans might start to degenerate. Similar fears were also widespread in Europe. In 1900, the London *Times* told its readers that 'An Empire such as ours requires as its first condition an Imperial Race – a race vigorous and industrious and intrepid. Health of mind and body exalt a nation in the competition of the universe. The survival of the fittest is an absolute truth in the modern world.'[9] The question was, were the British still a fit race? During the Boer War a high proportion of the recruits had turned out to be unfit for service; the squalor and disease of the urban slums in which they had been raised were widely blamed. Other critics were more concerned with the officer class, claiming not only that society's elite was going soft, but also deploring the fact that the birth rate among the elites was so low (why this was so remained a subject not fit for polite conversation, though knowledge of effective contraception was widespread). The result was that the less fit were outbreeding their betters, reducing the quality of the race as a whole.

While the British, characteristically, worried about class, the Americans were more concerned with race. The Statue of Liberty extends its welcome to the Old World's tired, its poor, its 'huddled masses yearning to breathe free', but also offers a home to the 'wretched refuse of your teeming shore'. But some were apprehensive that the new arrivals pouring in through Ellis Island were indeed Europe's rejects – lazy, stupid and immoral. Was the hardy pioneer stock that had tamed the wilderness becoming fatally diluted by mass immigration?

Not surprisingly, these anxieties led to a revival of interest in Galton's theory of eugenics. When he had first proposed it in the 1860s he had been widely mocked, but in 1904, Galton – by now a rather grand old man of seventy-eight – gave a public lecture on eugenics to the Sociological Society of London, drawing a large, influential audience. One result was the founding of the Eugenics Education Society, which publicized his ideas and promulgated the benefits of controlled breeding. The revival of Galton's ideas led to new answers to his old question: was it nature or nurture that defined character and behaviour? Britain's infant Labour Party and

its allies in the Liberal Party argued for nurture: the key to progress was eliminating poverty and improving the living conditions of the poor. But the eugenicists rejected this approach: Karl Pearson, the first occupant of the Galton-funded chair of eugenics at University College London, argued in 1909 that if the government were to 'Give educational facilities to all, limit the hours of labour to eight-a-day – providing leisure to watch two football matches a week – give a minimum wage with free medical advice', they would 'find that the unemployable, the degenerates and the physical and mental weaklings increase rather than decrease'.[10]

For many, the only way to resolve these arguments was through biology, by understanding the nature of heredity. The new science of Mendelism seemed to offer a solution: could controlled laboratory experiments finally prove, once and for all, whether you could choose to create a Prospero or a Caliban?

At Harvard, Professor William E. Castle, a modest Mid-westerner who was to become one of the century's most influential biologists, was one of many who took up this challenge. Castle was especially interested in the question of inbreeding: although repeated inbreeding was deliberately used by breeders as a way of 'fixing' a desirable trait, would this eventually prove harmful to the breed? Castle certainly found so when he carried out repeated brother-sister matings in rabbits – undesirable traits seemed to build up rapidly, eventually producing animals that were too sickly to survive. He was mainly interested in inheritance in mammals: mice, horses, rabbits and – as we will see – guinea pigs. However, in his efforts to find an organism that could withstand repeated inbreeding, he looked further afield, eventually settling on a creature that could survive twenty generations of close inbreeding with no loss of vigour – *Drosophila melanogaster*.

Castle's central focus remained on mammals, but several of his students took up the fly in the early 1900s and they were soon to be found in biology labs at Harvard, at Indiana University and at the Cold Spring Harbor Laboratory, where Frank Lutz, another of Castle's students, was using flies for work that was funded by the Carnegie Institution. It was from Lutz and Castle's other students

that Thomas Hunt Morgan, at this time still a supporter of de Vries's Mutation Theory, first learned how useful the flies could be. While some researchers latch on to a particular creature and work with it their whole lives, Morgan loved finding new organisms to work on; at various times he studied pigeons, Hawaiian land snails and Western song sparrows. As one of his colleagues joked, Morgan 'has more irons in the fire than an ordinary man has coals'.[11]

In 1907, when a new doctoral student in Morgan's lab at New York's Columbia University was interested in experimenting on the inheritance of acquired characteristics, Morgan suggested he tried using Drosophila probably, at least in part, because his lab was small and already crowded – and the flies were very small. Castle may well have had similar motivations: in 1910, his lab had 400 rabbits, 700 guinea pigs, 500 mice, 1,000 rats, 400 pigeons, eight dogs and more frogs than he could count. Flies were also cheap to acquire and keep, and Morgan was notoriously mean with institutional money (despite being very generous with his own). The student later recalled how he had obtained his first stock of flies: 'I used the simple procedure of laying some ripe bananas on the window sills; the flies thus caught were the start of my experimental work.'[12] The long-established relationship between bananas and Drosophila was about to acquire a new partner, biologists. Together, they would do astonishing things.

Mutation hunting

The relationship between flies and biologists is an example of what is sometimes referred to as pre-adaptation: a clumsy term, but one that describes an important phenomenon. Sometimes a species that evolution has shaped for one environment proves – purely by accident – to be ideally suited to an entirely new one. As the historian Robert Kohler has shown, Drosophila proved to be pre-adapted to academic biology labs: the flies are plentiful in the autumn – the beginning of the academic year – thanks to rotting fallen fruit. As long as they were kept indoors and warm, the flies continued to breed throughout the winter – producing a new

generation every couple of weeks – and bananas provided a cheap, convenient source of food. Best of all, especially for those trying to teach biology, if a careless student killed them off, Drosophila were inexpensive to replace; colonies of larger animals, by contrast, were far too valuable to be entrusted to inexperienced students.[13] Morgan found that the flies made especially good New Yorkers since they were happy to live in tiny, cramped apartments: dozens of flies would live and breed happily in an ordinary half-pint milk bottle, which gave them another advantage – Morgan and his students could 'liberate' a few milk bottles from their neighbours' doorsteps on their way into the lab in the mornings, so the cost of keeping flies was little more than the price of a few bananas.

At the time Morgan entered the fruit flies' story he was, as we have seen, an advocate of both the Mutation Theory and the European style of laboratory biology. In 1904 he married one of his former graduate students, Lilian Vaughn Sampson, daughter of a wealthy Philadelphia family. They spent their honeymoon at marine research labs in California, where Morgan spent the summer studying the shift from asexual to sexual reproduction in aphids. At the end of the summer they moved to New York, so that Morgan could take up his new post at Columbia's zoology department, working alongside his friend Edmund Beecher Wilson, who was chair of the department.

Columbia proved the perfect place for Morgan, because a key step towards understanding chromosomes, the still rather mysterious 'coloured bodies' of the cell nucleus, had been made in Wilson's lab at Columbia by one of his graduate students, Walter Sutton. Sutton was a farm boy from Kansas, where he and his teacher Clarence McClung had made a small contribution to reducing the state's abundance of grasshoppers by using them as a standard organism for work on cells and chromosomes; they had discovered that the large lubber grasshoppers (*Brachystola magna*) had very large testicles (by insect standards), making them easy to study. Sutton took his grasshoppers to Columbia with him, where he hoped to use them in investigating the connection between

chromosomes and inheritance that had been suggested by several distinguished European biologists.

Sutton showed that the behaviour of chromosomes during cell division clearly mirrored the evidence from Mendelian breeding experiments. His argument centred on the suggestive fact that when viewed under a microscope, the normal body cells of an organism all have their chromosomes arranged in pairs that are similar but, as we shall see, not quite identical. Normal body cells are referred to as diploid (from two Greek words meaning 'double form'); in *Drosophila melanogaster* each cell has four pairs of chromosomes, giving eight in total. As a plant or animal grows, each of its cells divides to create new cells, and each pair of chromosomes is duplicated so that each of the new cells gets a full set (and so every cell in the organism is diploid). However, the sex cells of an organism – eggs and sperm, or ova and pollen in plants – have only one copy of each chromosome (and are known as haploid, from 'single form'). When an organism's sex cells, or gametes, are being created a different kind of cell division occurs, in which the number of chromosomes is halved; in Drosophila, the eight chromosomes are reduced to four, one from each pair. Without this 'reduction division' (now known as meiosis) the number of chromosomes would increase, generation after generation; if each cell already contained a full set, the fused cell would contain two sets, in the next generation there would be four, and so on. Instead, the chromosome number in the gametes is halved, so that when the two haploid sex cells join during fertilization, the two half sets match up again to create a new full set. Obviously, half of the chromosomes in the newly fertilized egg have come from the ovum (the maternal chromosomes) and half from the sperm (the paternal chromosomes), and the fertilized egg is now diploid again, ready to begin growing by dividing. One final point about chromosomes is that they come in matching pairs; when gametes are formed, there is only one member of each pair of chromosomes in each gamete. For convenience, biologists normally number them, so Drosophila's chromosomes are known as chromosome 1, chromosome 2, and so on; when two gametes

fuse, chromosome 1 from the father pairs up with chromosome 1 from the mother, and the same applies to each of the other chromosomes.

While Sutton was in the middle of working out what was going on with his grasshoppers' chromosomes, William Bateson visited New York to promote the newly 'rediscovered' Mendelian theory. Listening to Bateson speak, Sutton suddenly saw how Mendel's principles related to his work; the behaviour of the chromosomes mirrored the behaviour of the still-hypothetical Mendelian factors. When he published his experiments, he noted 'the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reducing division as indicated above may constitute the physical basis of the Mendelian law of heredity'.[14] Sutton took his results to Wilson, who was initially baffled, then stunned as he realized their implications: if Sutton was right, chromosomes must indeed be the physical location of the elusive particles of inheritance.

When Morgan arrived at Columbia, he found that Wilson and one of Morgan's own former graduate students, Nettie Stevens, were working independently on following up Sutton's work, by investigating whether chromosomes determined the sex of the offspring, a topic that intrigued Morgan. The key seemed to lie in a mysterious chromosome, which McClung had first identified, which appeared not to have a pair and so was referred to as the 'accessory chromosome'. McClung marked these mysterious chromosomes with an X in his drawings of them, which is how they got their modern name, the X-chromosome. McClung thought the accessory chromosome might determine the sex of the offspring and when Sutton found X-chromosomes in only one half of the grasshopper sperm he examined, he believed he had confirmed his teacher's theory. Since the males had an X-chromosome and the females did not, it seemed that this chromosome did indeed determine their sex. In fact, this turned out to be wrong, but it was a perfectly understandable mistake: grasshoppers are unusual in that the males have one chromosome fewer than the females (they have no Y-chromosome). A couple of

years later, Stevens identified the far more common pattern, which is that the X-chromosome does have a partner, the much smaller Y-chromosome. In most animals and plants, two copies of the X chromosome make the organism female, while one X and one Y make it male.

This all took a few years to unravel; in the meantime, although Morgan was intrigued by Sutton's work, he was still convinced that sex determination must be more complicated than this. Like so many of his contemporaries, Morgan was both fascinated and baffled by the problems of inheritance. He did not believe that ordinary continuous variations were inherited – such minor fluctuations were, he thought, most likely to be due to minor variations in the organism's environment. But even if continuous variations were inherited, they would soon be diluted until they disappeared. However, he realized that there were problems with saltationism too, since an organism that possessed one of the larger discontinuous variations (whether one called it a mutation or a saltation) would still need to find another organism to breed with; the chances of it finding a partner which possessed the same rare mutation must necessarily be small. As a result, Morgan concluded that with continuous *and* discontinuous variation, 'the swamping effect of intercrossing would in both cases soon obliterate new forms'.[15] Only a significant number of fairly large variations, all occurring together and all of the same kind, could overcome these problems. Finally, but perhaps most importantly, Morgan made the standard worm-slicer's objection that Darwinism could not be verified experimentally in a laboratory.

These were the objections that had persuaded Morgan of the value of de Vries's Mutation Theory. De Vries's mutations were qualitatively different from normal continuous variations (they were large enough to create some degree of infertility with the original, unmutated form, which protected them from swamping). Also, de Vries's hypothetical 'mutation periods' ensured that many mutations occurred simultaneously; there was thus a greater chance of two organisms with the same mutation mating – and passing that mutation on. Morgan seems to have first taken

an interest in Drosophila in the hope that the flies would finally provide clear evidence of de Vriesian mutations in a species other than Oenothera. When de Vries visited the United States in 1904, Morgan heard him speak about the strange new 'Röntgen' or X-rays produced by the decay of that equally mysterious new substance, radium.[16] Perhaps they might produce artificial mutations in plants and animals? This suggested a new approach to identifying mutations and Morgan did some experiments, including some on insects, but did not get any results he thought worth publishing and dropped the idea.

A few years later, Morgan once again tried inducing de Vriesian mutations artificially. He now subjected Drosophila to acids, alkalis and other chemicals, varied their diets and conducted more radium experiments. The results were still disappointing, so Morgan tried another approach. One of de Vries's hypotheses was that intense selection – such as would be caused by a dramatic change in living conditions – could induce a mutation period. It may have been this idea that prompted Morgan to try large-scale breeding experiments with his flies.

The flies bred enthusiastically, so much so that Morgan soon complained he was 'head over ears' in flies and recruited some undergraduates to help out. In the fall of 1909 he taught the introductory biology course at Columbia – for the one and only time in his career. Among his students were Alfred Henry Sturtevant and Calvin Blackman Bridges. Despite not being a particularly effective lecturer, Morgan managed to convey – to these two at least – the excitement of biological research, and communicate a sense of the vital problems still to be solved. It was his personality, rather than what he said, that persuaded them both to approach him and ask if they could help in his lab. Morgan accepted their offers gratefully. Sturtevant rapidly became Morgan's favourite student; his father bred horses on a farm in Alabama and he had written a paper on the inheritance of coat colour in horses, which had impressed Morgan so much that he gave Sturtevant his own desk in the lab. Knowing Bridges needed money, Morgan hired him as a bottle-washer, cleaning

the rotting banana and dead flies out of the purloined milk bottles, ready for the next experiment.

However, Morgan and his 'boys' – as Sturtevant and Bridges soon became known – faced an unusual problem when they started their breeding experiments: not being a domesticated species, Drosophila had no well-defined, clearly visible characteristics to select for – they all looked pretty much alike. By contrast, human 'fanciers' had lovingly cherished and bred animals such as dogs and pigeons to create well-marked and unusual characteristics, such as extravagant tail feathers. So Morgan's team became the world's first fly-fanciers: they selected a visible characteristic, a pattern on the fly's thorax (its chest region) that looked like a trident, and began selective breeding, crossing large tridents with large tridents, and small with small.

Morgan's early experiments with Drosophila seem to have been intended to push the flies into a mutation period like the one de Vries believed he had observed in Oenothera. But the hoped-for mutations failed to appear and after a couple of years Morgan was on the brink of losing interest when, in January 1910, a much darker trident, pattern appeared. Finally, a mutation, which Morgan dubbed '*with*'. The mutant fly appeared at about the same time as Morgan and Lilian's third child (a daughter who was also called Lilian). When Morgan went to meet the new arrival in hospital, his wife's first question was, 'Well, how is the fly?' He launched into an excited description of his research and it was several minutes before he remembered to ask 'And how is the baby?'[17] Thirty generations later, in November of the same year, an even more pronounced mutant – *superwith* – showed up; various others had been spotted in the intervening months: in March a mutant with a dark blemish at the junction of wing and thorax – *speck* – had appeared and the body-colour mutant – *olive* – emerged in the same month. May saw the arrival of *beaded* wing, and a different *olive* body-colour mutant. Morgan quickly produced a paper claiming that – for the first time – a de Vriesian mutation period was under way in a species other than the evening primrose.

However, just as the flies seemed to be confirming de Vries's approach, doubts set in. These new 'mutants' were not in fact mutants, at least not in the sense de Vries had used the term. A genuine de Vriesian mutation was supposed to be a major jump, possibly large enough to produce a new species in a single leap (de Vries was always a little vague on this point). A large enough leap would produce a new organism that could no longer interbreed with the old version, thus allowing it to be defined as a new species: it was the survival of the Oenothera mutants alongside the parental forms, resisting blending and swamping, that had first excited de Vries. Yet Morgan's mutants were different. They were definitely leaps – not examples of the smooth, continuous variations of classical Darwinism – but the jumps seemed too small. Also, the new mutants could be successfully crossed with each other, so they could not be considered new species.

The new, small mutations might not be what de Vries had in mind, but they provided Morgan's fly workers with a glimpse of the still mysterious Mendelian 'factors' at work, most of which were normally hidden. Take eye colour, for example: human eyes come in many colours, whose patterns of inheritance allow us to deduce something about the factors involved, such as the fact that the factor for blue eyes is recessive to that for brown. But all Drosophila have red eyes, so Columbia's fly fanciers could not say anything about the inheritance of eye colour in flies until a new mutant showed up – which indeed it did: one that had white eyes. When a male *white* mutant was crossed with a normal red-eyed female, Morgan got a whole generation with red eyes, but when he crossed these, he got three times as many reds as whites in the next generation. Despite his scepticism about Mendelism, Morgan had done some mouse-breeding experiments a few years earlier to test the theory, so he knew a Mendelian ratio when he saw one: not only was the *white* mutation not a new species, it was clearly behaving like a standard Mendelian recessive factor. Although other labs were working on Drosophila, no one had seen the Mendelian ratio before, partly because the flies lacked clear characters, comparable to the yellow and green colour in

peas, which could have been easily contrasted. Just as Mendel had carefully selected his peas to produce clear-cut characters for his experiments, Morgan and his boys had begun remaking the fly into something that could be used for experiments, and the mutations were what made this possible: *white* revealed patterns of inheritance that could not have been observed in wild flies. As the fly workers selected and bred flies with visible mutations for their work, a wild organism was being domesticated – turned into a tool.

Morgan recognized that he was on to something interesting and was intelligent enough to admit that he had been wrong about the Mutation Theory, which he quickly dropped, starting to follow up his new Mendelian leads instead. Back in Europe, de Vries had reason to be concerned. The Mutation Theory seemed to be crumbling; when Morgan called his tiny *white* fly a 'mutation', he knew that however enthralling it was, it clearly was not what de Vries would call a mutation.

Mass production

As the flies bred and mutated, Morgan's lab, on Manhattan's Upper West Side, was transformed from a general-purpose biology laboratory – full of starfish, pigeons, mice and a host of other creatures – into a factory, a production line for churning out Drosophila. It became known as the fly room. Compared with Henry Ford's new 2,000-acre car factory at River Rouge, which was being built at about the same time, the fly room was tiny, roughly 16 by 23 feet (accounts differ). But the fly room's eight desks were as devoted to modern, standardized mass production as Ford's assembly lines.

In the early twentieth century, America was rapidly learning the benefits of standardization. The individual brilliance of the previous century's heroic inventors, men like Thomas Alva Edison, was admirable, but light-bulbs were useless without a system for generating and distributing electric power, and that involved defining and setting standards for everything from wires to voltages. The power grid allowed electric motors – which were

smaller, cleaner and more flexible than steam engines – to be used in factories. It was that flexibility which made Ford's production lines possible: instead of arranging the machinery and the workers around massive, noisy steam engines, electric motors allowed the machines they powered to be arranged according the stages of a car's production. Each type of car component was identical, built from standardized parts, with one section of a standardized conveyor belt devoted to each assemblage; electricity made it possible for raw materials to flow into the factory at one end, while cars flowed out the other.

In 1911, as new mutants were appearing up in the fly room, Frederick Winslow Taylor published his *Principles of Scientific Management*, a book that exemplified the new spirit of business efficiency. It was an immediate success, quickly translated into half a dozen languages, and it carried Taylor's message of 'scientific management' around the world. He argued that every business needed to be reshaped like a machine, each individual worker becoming a small, standardized and easily replaceable part. As he put it, 'in the past, the man has been first; in the future the system must be first'.[18] It was a creed that horrified labour leaders and trades unionists, for whom 'Taylorism' encapsulated the soul-destroying tyranny of mechanized mass production: labour without skill, creativity or pause for breath. But for manufacturers, Taylorism offered the prospect of vastly increased productivity and profits.

Taylor, though coming from a wealthy Philadelphia family, had chosen to work in the Midvale Steel Company's machine shop, originally because his doctor had recommended manual labour for his health. He was deeply impressed by the company's president, William Sellers, a prolific inventor who had helped devise the screw threads used in all American factories. The Sellers thread was promoted as the perfect example of the benefits of standardization: instead of every machinery maker and factory-owner having his own screws precision cut by master craftsmen, agreed standards allowed millions of identical screws to be cheaply mass-produced.

Taylor's gospel of scientific management and standardization caught the imagination of Milton J. Greenman, director of Philadelphia's Wistar Institute for Medical Research. Greenman decided that Taylor's system of time management could be applied to research labs, just as easily as to factories. He took the Sellers thread as a model of the virtues of standardization; 'such standards', he wrote, might 'result in immense economies in science as well as in commerce'.[19] Greenman set-out to Taylorize the Wistar Institute's rat colony, to produce standard, experimental rats by standard methods. By 1912, Wistar was to rats what United Fruit was to bananas: it was turning out over 6,000 of its carefully bred 'standard' rats a year and shipping them all over the country.

The Wistar rats showed American scientists what was possible when an organism was mass-produced. With standard rats came standardized data: the rats were supplied with a copy of the Institute's book *The Rat: Data and Reference Tables* (1915), the operating manual for the Wistar rat. No comparable statistics existed for any other animal, even humans. This allowed the results from one lab to be readily compared with those from another. Mass-produced animals would push the laboratory revolution further and faster than anyone could have imagined.

Morgan's fly room, funded in part by the Carnegie Institution, certainly did not look anything like one of Taylor's scientifically managed modern factories: the desk drawers were full of cockroaches, living off the Drosophila food, the whole place was chaotic and noisy, filled with the buzz of flies and talk about flies. Morgan's team had had no intention of getting into the mass-production business, yet – despite the racket and the squalor – Columbia's fly production soon outstripped both Wistar and River Rouge. It became clear that what the fly room was witnessing was not a de Vriesian mutation period at all; the rapid discovery of new mutants was simply the result of mass production, a reflection of the sheer numbers of flies involved. No one had noticed these small but distinct mutations before because they were rare. If only one fly in 100 produced a mutation,

mutations were unlikely to show up in an experiment with only 100 flies; in a colony of thousands, they become common and patterns of mutation become obvious. That was also why the early experiments with acids and radiation had apparently not produced results. More flies meant more mutants. More mutants meant more publications, more prestige, more graduate students to carry the fame of the fly across the world, and more honours, funding and publicity for Columbia's fly workers.

Morgan was Drosophila's Henry Ford, presiding over a mass-production system that turned out new research papers almost as quickly as it turned out flies, but Calvin Bridges was the fly room's Frederick Taylor. While Henry Ford always denied any debt to Taylor, Morgan and Bridges formed an ideal team, although Morgan did not always realize it. As we have seen, he made a virtue of making do with inexpensive, improvised equipment; Bridges loved to tinker, constantly looking to improve the fly room's efficiency, as if intent on increasing the fly-hours worked.

Bridges's ingenuity was applied to every aspect of the fly production line. In the early days of the fly room, when a researcher wanted to trap a single interesting fly, he would take advantage of the fact that Drosophila move instinctively towards light. A researcher would have to take the top off a bottle swarming with flies, hoping the target fly did not escape in the process, and slap a clean bottle upside down on top. Then he would hold the bottles up so that the light shone through the bottom of the empty bottle. Gradually, the tiny insects would crawl towards the light, into the new bottle. As soon as the target fly was in the new bottle, it was capped. The process was then repeated, over and over again, until the target fly was isolated (or had escaped in the process). This tedious process outraged the engineer in Bridges. He discovered that a carefully measured dose of ether was enough to knock the flies out for a few minutes, so that specific flies could simply be picked out and placed in a new bottle before they came round. Not content simply to pour ether over his flies (too much would kill them), Bridges designed a fly-etherizer, which gave the flies a carefully measured dose.

As in other factories, the workers in the fly room went on strike when the place got too hot or too cold; cold weather stops Drosophila breeding, high temperatures can kill them. So in 1913 Bridges turned some old bookcases, incandescent lights and thermostats into constant-temperature cabinets. A few years later he constructed improved versions, with ventilation and humidity controls. Never able to resist a chance to improve things, he introduced further refinements in 1930, and his home-made cabinets were still substantially cheaper than commercial incubators. He also built the first fly morgues (to dispose of dead flies). However, even with all Bridges's improvements, a state-of-the-art fly room in the mid-1920s was much cheaper to equip and run than a guinea pig colony or a plant-breeding station.

Although Bridges's ingenuity saved both time and money, Morgan was a little dismissive of what he called the 'folderol' that Bridges was constantly introducing into the work – such as the sophisticated binocular microscopes that were replacing the hand lenses Morgan preferred. Ignoring Bridges's elegant fly morgues, Morgan simply squashed flies that carried no interesting mutations on his desk or notebooks. He also rejected the etherizer, preferring to simply pour ether on the flies and risk killing them, but the other fly workers were more appreciative.

Standard flies and fly people

So, what exactly were Morgan and his students doing with all these flies? When Morgan first experimented with the white-eyed fly, he had noticed something interesting – the white-eyed flies were always male. Careful crossings confirmed that the white mutation was always linked to the sex of the fly. That was interesting because of its implications for Morgan's work on sex-determination; it suggested a connection with the work Wilson and others had done on chromosomes. One of Morgan's initial objections to the idea that chromosomes might carry the hereditary factors was that the flies have far more visible characteristics (such as eye colour, body colour and trident pattern) than they have chromosomes. If the hereditary factors

were located on the chromosomes there would have to be several on each one, in which case all the factors on a single chromosome would always be inherited together. The connection between eye colour and sex suggested exactly the kind of physical linkage, or 'coupling' as it was initially known, that the chromosome theory would predict. Within a year, Morgan had found two more examples of what he called 'sex-limited' mutations: one for yellow body colour and one for miniature wings. One link might be a coincidence, but three seemed to prove that factors were indeed inherited together, on the same chromosome.

But no sooner had linkage been discovered than it began to break down. Factors that were normally linked were sometimes inherited separately. Intriguingly, for any given pair of factors the frequency with which linkage broke down was constant, but it varied between one pair of factors and another. For example, factors A and B – which were almost always inherited together – would separate in 1 per cent of crosses, while factors C and D, also usually linked, separated 2 per cent of the time. As Morgan's team struggled to understand this anomaly, they were able to draw on an increasingly comprehensive body of work on chromosomes, whose role in heredity was gradually becoming clear.

In 1909 Morgan read a paper by Frans Alfons Janssens, a Belgian Jesuit priest and gifted microscopist, who taught biology at the Flemish University of Leuven. Janssens's short paper simply described what he had seen under his microscope: chromosomes did some very odd things during meiosis. Before their final reduction into half-sets, they wrapped themselves around each other and appeared to break apart and rejoin. Janssens's phenomenon was christened 'crossing-over'. Morgan and his students suggested that crossing-over explained the occasional breakdown of linkage. They pictured the hereditary factors rather like beads strung along the chromosome. During crossing-over, the two chromosome necklaces – one originally inherited from the father, the other from the mother – broke at random points and then joined again. If the chromosome the fly inherits from its father is pictured as a string of green beads, and that from its

mother as a string of red beads, after crossing-over, there might be a green string with a few red beads at one end, while the red string had acquired a few green beads; this was how linked factors sometimes got unlinked. If crossing-over was random it would produce a different mixture of red and green on each of the fly's four pairs of chromosomes. However, the crucial point was that the closer together any two beads were, the less likely it was that a random break would occur in-between them; the further apart they were, the greater the chance of a break. If two of the hereditary beads were close together on the chromosome, they would almost always be inherited together, providing strong linkage, but if they were far apart, they would be separated so often that they almost appeared to be inherited independently of one another. As Morgan wrote, that was why 'we find coupling in certain characters, and little or no evidence at all of coupling in other characters; the difference depending on the linear distance apart of the chromosomal materials that represent the factors'.[20]

Inspired by this idea, Morgan and his students began to look for mutations that were usually linked. As they searched, they discovered that the mutations fell into four distinct 'linkage groups'; the fact that *Drosophila melanogaster* had four pairs of chromosomes made it overwhelmingly likely that each linkage group corresponded to a pair of chromosomes. By 1914, it was clear that the Mendelian theory and the chromosome theory were not rivals, they were one and the same: the Mendelian factors were real and they were located on the chromosomes. As this became increasingly accepted, the carefully neutral language of 'factors', which had been used before anyone knew what they were dealing with, was gradually dropped and a new term, 'gene', came into use. By 1917, Morgan and his group were using it and soon everyone was referring to the study of inheritance as 'genetics' (a term coined by Bateson) and the people doing it as 'geneticists'. Even though no one yet knew how these genes actually worked, the new language reflected geneticists' growing confidence that they were working on a tangible, physical phenomenon whose precise nature would, sooner or later, be fully understood.

Once the connections between linkage, crossing-over and chromosomes were understood, the flies were put to a brand-new use. Sturtevant, still just nineteen-years-old, realized that the frequency with which two genes crossed over could be used to estimate how far apart they were. The fly workers were now going to persuade Drosophila to help them work out precisely where on each chromosome each gene was, to fix the position of each bead on the string. Sturtevant took Morgan's data home one night in winter 1911 and came back to the lab the next morning with the first, basic chromosome map. The following year, Morgan set him and Bridges the task of mapping all the fly's chromosomes.

The principle of mapping was simple: mutations were a tool that allowed the fly boys to see what was happening to each gene in a cross, but to take advantage of them, careful breeding was needed to create a stock of flies that combined a specific pair of mutations. Once that was done, cross-breeding stocks with particular combinations of mutations revealed the frequency of crossing-over – by simply counting the flies' offspring and observing how many times the genes remained linked and how often they were separated. Bridges had unparalleled patience for this kind of work, sitting at a microscope for hours at a time, counting thousands of flies while looking out for new mutants. However, the frequency simply revealed whether the genes were close together or far apart. The next step was to try to translate that into a precise distance: to determine exactly how far apart on their chromosome the factors lay. Doing this required three genes, A, B and C. They were usually inherited together, so they were on the same chromosome, but – thanks to crossing-over – the links sometimes broke down. The data showed that A and B were more closely linked (i.e. closer together on the chromosome) than A and C (because the link between A and B broke less frequently than that between A and C). The same was true for B and C – they were also closer together than A and C. That suggested that B was somewhere in between A and C. To test this, a researcher would carefully measure how often A and B crossed over, and then do the same for B and C (which took two sets of time-consuming,

tedious experiments). Adding the frequency from A to B to that from B to C gave a prediction of how often A to C ought to cross over. That estimate could then be checked using a third experiment.

Similar sets of experiments needed to be done for every identifiable factor on each of the four chromosomes, but thanks to the speed with which the flies bred, the relative positions of the genes along each of the chromosomes were gradually worked out. If that all sounds mind-numbingly tedious, it was: the chromosome maps produced between 1919 and 1923 used data from between 13 and 20 million flies, every one of which had to be selected, cross-bred, etherized and counted. Although a single fly is only a couple of millimetres long, if all these flies had been laid end-to-end, they would have formed a line of flies over thirty-five miles long. The efficient, mass-production techniques developed in the fly room were essential; without them, the work could never have been done.

However, even this description of the work does not begin to capture the labour involved. The basic mapping technique assumed that crossing-over was uniform along the chromosome – that it was equally likely to break at any point along its length – but that proved not to be the case. As Sturtevant and Bridges mapped, they kept getting anomalous results. Investigating these resulted in the discovery of many types of genes whose existence no one had suspected: such as genes that had no visible effect on the fly, but reduced the rate of crossing-over. Sometimes a useful, visible mutation occurred too close to one that made the flies weak, or even killed them. Months of frustration could result and many more months would be needed to breed new Drosophila stocks without the troublesome gene.

As the work continued, something remarkable was taking place in the fly room. The wild fruit flies were not merely being domesticated, they were being rebuilt into standardized organisms, as standardized as the Wistar rats or Sellers-thread screws. The flies were 'cleaned' of unhelpful genes that complicated the experiments; once the problematic gene had been detected, a new

stock of flies would be created through careful cross-breeding, as it would if a stock were found to be too slow-breeding, or susceptible to disease. Anything that slowed down the work was bred out. In the process, the fly boys were learning a great deal about genes, but they were also building a new kind of fly, one that was an amalgam of genes from many different wild varieties of the insect. The fly room eventually contained nearly 400 unique lab-bred stocks, each cleaned up so that it combined a precisely selected combination of mutations; each stock was both an appealing object of study and also a tool, a genetic probe, that could be used to investigate the genes of an unknown fly.

As the standard fly was constructed, its value as a laboratory tool rose and the fly people began to value and respect it more. In the early days of the research, they often complained of being smothered in pesky flies, but such observations gradually faded; Drosophila was even referred to as 'that noble animal' by one worker.[21] In their early papers, many researchers omitted to mention that they had brought colonies of these rather revolting little insects into their labs, but as the fly showed what it could do, the geneticists who worked on it began to identify themselves as a community, referring to themselves as 'fly people' or 'Drosophilists'.

Have flies, will travel

The unique atmosphere of the fly room attracted much interest, initially within Columbia itself, but eventually all over the world. Everyone who visited commented on the fly room's informality and the air of excitement it generated. Sturtevant later wondered 'how any work got done at all, with the amount of talk that went on'.[22]

Sturtevant was especially interested in theoretical issues, while Bridges was in charge of giving away the carefully constructed stocks of Drosophila. One of the great advantages of working with flies was that they were cheap and portable; they took up so little space that an entire breeding colony could be transported in a bottle, and it was easy to simply give them away to researchers

who wanted to do their own experiments. Gifts of flies were an important part of making Drosophila into a standard organism, just like the Sellers-screw thread; a standard is no use unless everyone is using it. It became clear very early on that the flies could produce interesting problems so rapidly that there would be more than enough work to keep Morgan's team busy; giving away flies helped establish a community who would share what they knew and solve problems more rapidly. But it was no good distributing flies if people could not use them, so along with the flies, the Morgan group passed on what they knew about them. Bridges in particular was happy to teach anyone who was interested, all the tricks and techniques he had invented to keep the flies breeding. Eventually a printed newsletter – the *Drosophila Information Service* – was produced to help record and spread the essential fly lore. Freely exchanging flies and information about them became one of the unwritten rules of the fly community; the Drosophilists decided that it was in everyone's interest to share, and researchers who were disinclined to were quietly cut out of the network.

Among the many visitors to the fly room was Hermann Joseph Muller, a masters student from Columbia's physiology department, who started dropping in on Sturtevant and Bridges every Thursday. That was his one free day, since he had to support himself financially by teaching embryology to undergraduates and English to foreigners, and by working as a hotel clerk. He began to attend the fly room's evening reading groups, where new ideas were discussed over cheese and beer at Morgan's house. Muller found the fly group's work thrilling; Sturtevant recalled that the night on which he revealed the first chromosome map, Muller literally jumped with excitement.

Muller was born in New York, the grandson of a migrant metal worker, a bright, hard-working boy who had been top of his high-school class and won a scholarship to Columbia. He was soon fascinated by biology and organized an undergraduate biology club, through which he met Sturtevant and Bridges, who told him about the fly room. Although Muller was eager to join the

Drosophilists, there was initially no space for him in Morgan's lab.

Morgan, Sturtevant and Bridges were easy-going, much given to self-mockery and joking, but Muller took himself very seriously. His personality and late arrival made him feel like an outsider in the fly room, a feeling exacerbated by his tendency towards rigid opinions and ideas. Morgan was a humanitarian middle-of-the-road conservative, horrified by extremism of all kinds, but basically uninterested in politics. By contrast, Muller was a political radical, attracted to Marxism and communist ideas. Both scientifically and politically, Morgan seems to have regarded Muller as a bit of a zealot, while Muller came to feel that his contributions were often overlooked, with others getting more credit. The fly room's informality meant that everyone shared their ideas freely, but formal acknowledgement – in the shape of getting your name on a publication – went only to those who had done the actual experiments. Muller gradually began to suspect that these unwritten rules had been devised by Morgan and Sturtevant to deprive him of his fair share of recognition. However, Muller probably suffered because he was a quick thinker, but a slow worker: he produced ideas much faster than results, working away methodically at incredibly complex, sophisticated experiments that took years to complete. Meanwhile, the others took advantage of his ideas to get their work done first. Muller helped create many of the fly stocks the others used, including some of the trickiest ones, and eventually he came to resent Morgan, in private at least, feeling that the latter had hindered his career.

Morgan, who came from old Southern stock and had a somewhat aristocratic manner, and his golden boy, Sturtevant, who was clearly Morgan's favourite, bore the brunt of Muller's resentment. Calvin Bridges was largely exempt, partly because of their shared political views – even though Bridges' communist sympathies were arguably more a matter of affectation than of deeply felt conviction. Muller also seems to have regarded Bridges as an exploited blue-collar worker on the Drosophila shop-floor: he did the practical work of maintaining the fly stocks, while Sturtevant became more of a theorist because his colour-blindness made him poor at spotting mutants.

In 1917, while the fly work was at its height, the Russian Revolution had created the world's first avowedly socialist country. Like many young Westerners at the time, Muller viewed it as a heroic, idealistic revolt against a corrupt, undemocratic regime; Stalin's gulags and show trials were still years in the future. The revolution enthralled him, and in 1922 he decided to visit the Soviet Union, eager to see the new communist society for himself and to meet Soviet biologists.

The USSR was only five years old at the time, a fragile experiment still struggling to survive after a bloody civil war and a series of devastating famines. There were shortages of almost everything, so Muller – like any polite visitor – brought his hosts a gift, thirty-two small bottles. But instead of duty-free alcohol, they contained live Drosophila, samples of the fly stocks he had helped create. One might imagine that acquiring American fruit flies would not have been high on the Bolshevik government's list of priorities, but Muller's Soviet colleagues were thrilled. Lenin's regime took a great interest in science, especially biology. Inspired by the vision of Marxism as a scientific theory, which promised its adherents the power to reshape the world for the better, the Bolsheviks poured money into sciences such as plant- and animal-breeding, hoping to create better crops and animals, to avert future famines.

Muller met the leading Soviet geneticists, including Nikolai Vavilov, head of Moscow's gigantic Institute of Applied Botany, who had studied genetics in Britain with Bateson. However, it was another Nikolai, Nikolai Kol'tsov, who initally showed the greatest interest in Muller's ideas.

Before the revolution, Kol'tsov had been a liberal critic of the Tsarist government, which had cost him his job at Moscow University. He had managed to persuade a Russian railway millionaire to fund a new Institute of Experimental Biology (which became known as the Kol'tsov Institute), dedicated to Kol'tsov's vision of a new biology, which would bring together the science's great nineteenth-century achievements and combine them with newer ideas of Mendelism, biometrics and chemistry.

Inspired by the laboratory revolution, Kol'tsov encouraged his students to master lab techniques, but – more unusually – he also made sure they went out into the field and observed living creatures in the wild.

Kol'tsov invited Muller to give a talk on the American Drosophila research at his institute, and published a Russian translation of it. When Muller returned to the United States he left a stock of flies so that the Institute could develop its own Drosophila research. But Kol'tsov had a problem – there was no one at the Institute who knew anything about insects. So he turned to an old friend, Sergei Chetverikov, an entomologist who had studied with him at Moscow University.

Chetverikov must have seemed an unlikely figure to head a genetics programme: not only did he know almost nothing about genetics, he lectured on biometrics – most biometricians were hostile to Mendelism – and he was also a field entomologist, not a lab worker. But he knew a lot about insects and that was enough for Kol'tsov, who decided that Chetverikov's interest in biometrics – far from being a disadvantage – was a sign that his friend was open to new ideas.

Chetverikov did indeed prove eager to learn. He and his co-workers decided that they needed to start by learning English, but rather than start with textbooks or novels, they decided to read the latest American genetics papers. They would divide these up between them, take them home, read and translate them, then meet up at each other's apartments in the evenings to discuss what they had learned. They were, in effect, learning two foreign languages at once: English and Mendelian genetics. Inspired, perhaps, by the close-knit groups around Muller and Morgan, the Russian fly workers also became a group, which became known as the *Droz-So-or* (an acronym for *sovmestnoe oranie drozofil'shchikov*, or 'the Combined Cacophony of Drosophilists'), a name that gently mocked the endless proliferating bureaucratic acronyms that adorned the new institutions of Soviet power.

In many ways, the *Droz-So-or* was just like the Morgan group, except that a third of Chetverikov's colleagues were women, in

sharp contrast to the 'boys' who dominated the American fly rooms. Like their American colleagues, some of the Russians became interested in studying and mapping chromosomes, but Chetverikov was more interested in studying the genetics of wild populations. Still somewhat sceptical of the relevance of laboratory work to wild populations, he set out to see if the Morgan group's small mutations could also be found in wild populations.

The Combined Cacophony of Drosophilists began to trap wild flies and cross-breed them with Muller's lab-grown flies to discover the hidden genetic make-up of the wild population. The lab flies were rather like chemical reagents, which are used to determine the chemical composition of an unknown substance because they produce predicable reactions. Chetverikov's group knew which genes the American flies contained, so by patiently catching, crossing and counting wild flies, they could deduce which genes were present. The crosses revealed that wild flies varied enormously, carrying all kinds of recessive genes that only became visible when crossed with other recessive stocks.

As we saw with Mendel's peas, if a plant had yellow peas, it could either have two copies of the yellow version of the colour gene, or one yellow and one green (because yellow is dominant while green is recessive). In the early twentieth century, these different versions of a gene became known as alleles (from the Greek word for 'another'). Bateson coined the terms that are still used to describe an organism's genes: those with two copies of the same allele were homozygous; while those with two different alleles are heterozygous. The only way to distinguish the two cases was to cross-breed your pea plant with one that you knew was homozygous (because green is recessive, plants with green peas must be homozygous): the ratio of greens to yellows in the next generation would make it clear whether your original plant had carried two copies of the yellow allele, or one yellow and one green.

Chetverikov's group could use this kind of information by crossing wild flies with laboratory stocks that were known to be homozygous for the recessive gene; the offspring of such a cross

would then reveal if the wild fly had also carried the recessive gene. Their experiment convinced them that wild populations contained considerable hidden variation. However, wild populations of flies could not be treated in the same way as laboratory populations in bottles. In the lab, mating could be controlled, so the ancestry of any individual fly could be known and the precise combination of genes it carried could be calculated. A laboratory fly was like one of Sturtevant's father's prize racehorses; its pedigree could be inspected in the stud book. Knowing that all the flies in a bottle shared a pedigree meant they shared a common set of genes. None of this was possible with wild flies, so Chetverikov began to apply some of the mathematical techniques he had learned from the British biometricians for understanding the genetics of wild populations. His knowledge of statistics allowed him to take a sample from the wild, perform experiments in the lab to determine their make-up, and then extrapolate mathematically – applying the results to the world beyond the lab. Chetverikov calculated how frequently different recessive traits might occur in wild Drosophila populations, guessing that when a fly with a particular gene became more or less common, this was presumably the effect of natural selection, since the gene in question had either improved or reduced the fly's survival chances.

Chetverikov published the group's initial findings as *On Certain Features of the Evolutionary Process from the Viewpoint of Modern Genetics* (1926), a prosaic title that concealed something extremely important: for the first time, the biometricians' understanding of Darwinian natural selection and the Morgan group's version of Mendelian genetics, which had been seen as *competing* interpretations of evolution, were presented as *complementary*. Kol'tsov was impressed, and referred to Chetverikov's work as a synthesis that had 'great theoretical interest, in as much as it connects experimental laboratory genetics with the problem of the evolution of organisms in nature'.[23] If Chetverikov was right, he had found what de Vries had been searching for: a way of removing evolution from the realm of speculation and bringing it into the lab. But initially almost no one outside the USSR knew of his work.

The end of *Oenothera*

While the Russians were finding new uses for Drosophila, the Americans were also making further discoveries. In 1918, Morgan wrote to de Vries, asking for his comments on a draft article describing an exciting new discovery – made by Muller – that was to prove crucial in resolving a key aspect of the Oenothera mystery.

The fly boys had discovered that in some cases a gene that normally performed some vital function in the fly could mutate into a form which simply did not work: a heterozygous fly (one that had one working and one non-working version of the gene) would be fine, but it would pass the non-functioning allele on to half its offspring. If any of the unfortunate offspring got two copies of the non-functioning allele (one from each parent), they would die. The story becomes even more complicated in cases where the fly carried two such genes, which is what Muller had discovered. Suppose gene one comes in two versions – *A* (the working version) and *a* (the non-working one); and so does gene two – *B* and *b*. The only organisms that will survive are those that have at least one copy of both working genes (they would have to be either *AA* or *Aa*, combined with either *BB* or *Bb*). Any flies that are homozygous for either of the recessive alleles (i.e. that have either the *aa* combination, or the *bb* one) died.

The problem was how to detect the lethal recessive genes. Normally, a recessive trait – like the green colour in peas – shows up because some offspring are homozygous for the recessive trait; they have two copies of the green allele and so produce green peas, but any flies with two copies of the recessive lethal allele simply died. When Muller came to count the flies from his carefully constructed cross-breeding experiments, the normal Mendelian ratios that would have told him that his flies carried a hidden recessive gene were all confused. Understandably, it took Muller a massive amount of work to understand what was going on in these complicated cases. Once he had solved the problem, he realized that the same thing must be happening in some of de Vries's Oenotheras. *Oenothera lamarckiana* proved to be a case of what Muller termed 'balanced lethal factors', which meant that

the plant looked homozygous (because no recessives showed up in the crosses) when it was in fact heterozygous (carrying the hidden lethal alleles). Such cases are so rare that they had not been detected previously (another effect of the fly room's mass production); de Vries had concluded he had found a new species when what he really had was a very unusual kind of hybrid.

Morgan described Muller's findings and their implications in his letter to de Vries and concluded, 'I venture to think that the *mutation* problem of *Oenothera* may find a very happy solution in the theory of balanced lethal factors.' In the margin of the manuscript, de Vries wrote the single word 'unhappy'.[24]

However, if Muller's discovery made de Vries understandably unhappy, the worst was yet to come. As the fly work unfolded, the idea of big mutations producing a new species in a single leap became increasingly implausible. The gradual unravelling of the mysteries of the chromosome made it increasingly obvious that Oenothera was a freak. Researchers in several countries discovered that the plant's chromosomes behaved in the most unusual way, so that the normal Mendelian rules broke down completely. Among those investigating the plant's chromosomes was Reginald Ruggles Gates, who, despite his enthusiasm for the Mutation Theory, was to play a key part in the theory's undoing. In 1906 he and Anna Mae Lutz discovered that the *gigas* mutant, the large and vigorous 'new species' of Oenothera de Vries had first discovered, had twice as many chromosomes as a normal *Oenothera lamarckiana* (twenty-eight instead of fourteen). Over the next few years this quickly proved to be a common phenomenon among the Oenotheras; many of the mutant forms had unusual numbers of chromosomes.

What had happened in these cases was that Oenothera's reduction division (meiosis) had failed to work properly: the number of chromosomes had not been halved when the plant was producing ova and pollen. Some of the sex cells remained diploid, so when pollination occurred the new plants got extra chromosomes. Such duplications are rare in animals, but more common in plants; the phenomenon is known as polyploidy (meaning 'multiple form').

Oenothera was one of the first polyploid plants to be identified; its fame ensured that a lot of researchers had worked on it, which helped to reveal polyploidy's significance. Recall that when gametes fuse during fertilization, the chromosomes from each parent have to match up to form the usual diploid pairs that are characteristic of the normal body cells. However, if two different species hybridize, their chromosomes do not match and so cannot form pairs; sometimes no offspring result, sometimes they produce sterile progeny. The classic case is of course the mule, the offspring of a donkey (*Equus asinus*, which has sixty-two chromosomes) and a horse (*Equus caballus*, which has sixty-four chromosomes); when a horse and a donkey mate, their chromosomes are unable to pair up and the result is that mules, despite being tough and sturdy, are sterile. However, in a plant where the chromosomes have already been duplicated during the production of pollen or ova – because the reduction division has not worked – there will be two copies of each chromosome in the fertilized ovum, so each chromosome will still be able to find a partner. The result is that the new hybrid plant is fertile, but only when crossed with other polyploid hybrids. If crossed with either of its original parents, sterility results. Since the new polyploid plants often look very different from their parents and will not interbreed with them, they appear to be new species – exactly what de Vries found in some of his Oenotheras. A similar phenomenon occurs in many species of Hieracium, which was the other reason their behaviour was so baffling to Mendel.

Polyploidy also turns out to be relevant to another of the fly workers' discoveries. As we have seen, Mendel's pea experiments had been done with pure-bred strains that possessed very clear-cut, contrasting characteristics, such as green or yellow peas, so the twentieth-century Mendelians tended to think of genes as being like switches – they turned some feature of an organism on or off. However, the fly work produced a much more complex picture. It gradually became clear that genes also affect what other genes do; sometimes, for example, bits of chromosome are duplicated during crossing-over, so that a fly ends up with two copies of a gene, and

sometimes two genes produce twice the effect of one. This effect can also occur in polyploid plants, which is why the *gigas* 'mutant', with twice the normal number of chromosomes, was larger and more robust than its parent plants: some of the genes that determined its size had been duplicated and so their effect was doubled. It turns out that the same thing has happened in some of the plants we rely on for food: common wheat, for example, has managed to accumulate no less than six sets of chromosomes; these duplications have produced a plant with much larger, more nutritious seeds – a feature that *Homo sapiens* has understandably found particularly attractive. A comparison of the plump, appetizing grains of wheat with the tiny, tough seeds of most wild grasses reveals the effects of polyploidy in action.

Polyploidy can also explain how bananas became the favourite fruit of toothless babies. Wild bananas are full of hard, black seeds, which make them virtually inedible to humans, but the ones we buy have no seeds at all. This is another effect of polyploidy; somewhere in their evolutionary history, banana chromosomes were duplicated – all modern, cultivated varieties have three sets of chromosomes, instead of two – which produces bigger fruit without seeds (because, like mules, they are sterile). This would appear to be an evolutionary dead end, but bananas are one of many kinds of plants that can reproduce themselves by sending out shoots or roots that can grow into entirely new plants; these are known as suckers – one of the phenomena Henslow lectured on. Luckily, one of our sweet-toothed and sharp-eyed ancestors noticed these seedless bananas and worked out how to grow them by taking advantage of their tendency to produce suckers.

The fly who loved me

Drosophila have continued to prove highly adaptable and they are still exploiting the warm, food-rich ecological niche of the academic research laboratory. But they have nevertheless had to cope with the changing seasons of scientific fashion. For a while, after the Second World War, it seemed as if the fly's days were over, as smaller, simpler organisms were preferred by researchers.

But fly populations recover rapidly after a bad season, and in the 1970s Drosophila became the focus of renewed interest as new kinds of genetic research became possible, as we shall see. Today, countless millions of these tiny flies continue to buzz away in labs all over the world, teaching beginners the essentials of genetics and helping Nobel Prize-winners understand how complex behaviours are controlled by genes. Despite all the extraordinary advances in scientific understanding and technology that have been made since the first flies landed on the first over-ripe banana on a lab windowsill, many of the basic tricks of the fly trade have remained the same. Students still have to learn how to get the flies living and breeding before they can do their experiments. As one recent handbook jokingly informs the would-be Drosophilist, 'the flies frequently require you to do an apprenticeship on any important project – they will not start to perform until they are certain you are serious'.[25]

Thanks to those who took the time to get serious about flies, the list of things they have taught us is almost endless. Resolving the precise connection between chromosomes and inheritance was perhaps the most important, but inspired by the success of the fly workers, who rapidly became scientific stars, researchers began to study chromosomes in all kinds of plants and animals. Gradually, the idea of genes as simple switches, that could only be on or off, began to give way to a more complex picture. One result, as we shall see in the next chapter, was that the seemingly sharp distinction between smooth continuous variation and abrupt, jumpy changes began to break down.

In 1915 Morgan and his students published *The Mechanism of Mendelian Heredity*, which summarized many of their discoveries. Thanks to the pace at which the flies bred, it had taken only a few years to assemble a mass of evidence to support their claim that the hereditary particles were on the chromosomes. They were not the first to suggest this, but they were able to provide better evidence than ever before, evidence that the Mendelian factors were at specific physical locations on specific chromosomes. The fact that their results came from laboratory experiments made

them even more persuasive, as did the fact that Morgan's team would happily send stocks of the relevant flies to anyone who wanted to check the results for themselves. But while the fascination with flies spread rapidly, not everyone was fully persuaded by the new ideas. In Britain, Bateson had his own theories about inheritance and resisted the American ideas for many years; his considerable reputation helped to slow the fly's British advance for many years.

However, the strongest opposition to the Mendelian chromosome theory came, as one might expect, from a few of the naturalists and field workers, especially from the biometricians. They complained that breeding flies in milk bottles and adjusting the temperature so that they bred continuously created entirely unnatural conditions; of course they mutated under such stresses, and so the results obtained had no bearing on wild flies. Morgan was, understandably, contemptuous of these criticisms. He observed that critics implied 'that results obtained from the breeding pen, the seed pan, the flower pot and the milk bottle do not apply to evolution in the "open", nature at large or to wild types'. However, if biologists were to give up these experiments, chemists and physicists should give up using spectroscopes, test tubes and galvanometers, since these were all 'unnatural instruments'. Morgan argued that 'the real antithesis is not between unnatural and natural treatment of Nature, but rather between controlled or verifiable data on the one hand, and unrestrained generalizations on the other'.[26]

Yet even the most sympathetic naturalists found it hard to see how the discoveries of the fly room could be applied to evolution in the wild. The fly experiments depended on creating pure-bred flies with known pedigrees; that seemed to be the only way experimenters could know what genes they were dealing with. Of course, had the naturalists known of Chetverikov's work, they might have understood its implications sooner, but Chetverikov never got to complete the experiments necessary to develop his ideas. His career was cut short after Stalin came to power and the USSR became an increasingly repressive society. Among the millions arrested during

the crack-downs and purges of Stalinist Russia was Chetverikov; in 1929 he was sent into internal exile, forbidden to visit Moscow or Leningrad, and forced to work as a schoolteacher. He was lucky, in that he survived and eventually died of natural causes, but he was unable to publish anything further on genetics.

For a while, Chetverikov's students continued his work, but the Combined Cacophony was eventually devastated by Trofim Lysenko, who gained control over Soviet biology during Stalin's regime. Lysenko rejected orthodox genetics in favour of a form of Lamarckism which claimed to be able to evolve plants much more quickly than Mendelian methods. Lysenko claimed his views were more Marxist than those he called bourgeois 'fly lovers', whose links with US genetics were well known. Lysenko instituted an assault on orthodox genetics and the country's political leaders began to support him during the new famines of the 1930s. He promised a rapid solution to famine and, with Stalin's support, he eventually acquired the power to virtually outlaw Mendelian genetics. Many geneticists disappeared, were arrested and, in some cases, were even executed.

After Chetverikov's arrest and the dispersal of the *Droz-So-or*, their work might have remained almost unknown outside the USSR, but for a handful of people who publicized it in the West. Among them was the British biologist J.B.S. Haldane, another left-wing sympathizer who visited the USSR in the 1920s and came away deeply impressed by the level of government support for science (still unheard of in the West). A few years later, Haldane met Chetverikov at an international genetics congress, arranged for some of the Russian work to be translated, and encouraged his British students to read it. Haldane became intrigued by the possibility of applying biometric tools to genetics, but working out how to do this was to require a lot of maths – and a lot of guinea pigs.

15. Quoted in G.E. Allen, 'Hugo de Vries and the Reception of the 'Mutation Theory'": 56–7.
16. E.B. Wilson, quoted in G.E. Allen, *Thomas Hunt Morgan: the man and his science* (Princeton University Press, 1978): 34–5.
17. M.J. Schleiden, *Principles of Scientific Botany: or Botany as an Inductive Science* (1849; Johnson Reprint Company, 1849 1969): 575, 80.
18. H. de Vries to C. Darwin, [15 October 1881]: P.W. Van der Pas, 'The correspondence of Hugo de Vries and Charles Darwin', *Janus*, 1970: 173–213: 200.
19. E. Zevenhuisen, 'The Hereditary Statistics of Hugo de Vries', *Acta botanica neerlandica*, 1998: 427–63.
20. H. de Vries, 'On the Origin of Species', *Popular Science Monthly*, 1903: 481–96: 491.
21. ibid.: 492.
22. H. de Vries, *Species and varieties: their origin by mutation*: 525–6.
23. H. de Vries, 'On the Origin of Species': 494.
24. H. de Vries, *Species and varieties: their origin by mutation*: 28–9.
25. ibid.: 549–50.
26. ibid.: frontis.
27. H. de Vries, *Mutation Theory*, I: 5–6, quoted in G.E. Allen, 'Hugo de Vries and the Reception of the "Mutation Theory"', *Journal of the History of Biology*, 1969: 55–87: 59–60.
28. H. de Vries, *Species and varieties: their origin by mutation*: 28–9; G.E. Allen, 'Hugo de Vries and the Reception of the 'Mutation Theory"': 62–3.
29. C.B. Davenport, '[review of] Species and Varieties, Their Origin by Mutation', *Science*, 1905: 369–72: 369.
30. K. Pearson, 'Mathematical Contributions to the Theory of Evolution. On the Law of Ancestral Heredity'. Proceedings of the Royal Society of London, Vol. 62 (1897–1898), pp 386–412
31. [Anon.], '*Oenothera* and Mutation', *Nature*, 19 August 1915.
32. H. de Vries, *Mutation Theory*, I: 5–6. Quoted in G.E. Allen, 'Hugo de Vries and the Reception of the "Mutation Theory"': 59–60.

33. Quoted in J. Sapp, *Genesis: the Evolution of Biology* (Oxford University Press, 2003): 132.
34. H. de Vries, 'The Evidence of Evolution', *Science*, 1904: 395–401: 400.
35. S.E. Kingsland, 'The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900–1912', *Isis*, 1991: 479–509: 486–8.
36. C.H. Merriam, 'Is Mutation a Factor in the Evolution of the Higher Vertebrates?', *Science*, 1906: 241–57: 242.
37. ibid.: 243; G.E. Allen, 'Hugo de Vries and the Reception of the "Mutation Theory"': 68.
38. G.E. Allen, 'Hugo de Vries and the Reception of the "Mutation Theory"': 74–5.
39. H. de Vries to W. Bateson, [20 October 1901]. Quoted in B. Theunissen, 'Closing the Door on Hugo de Vries's Mendelism', *Annals of Science*, 1994: 225–48: 248.
40. [Anon.], *Athenaeum*, 28 August 1915.
41. 'F.L.', *Botanical Journal*, October 1915.
42. R.R. Gates, 'Review of "The Mutation Theory"', *American Naturalist*, 1911: 254–6: 255–6.
43. *The Times*, Monday 13 August 1962. Homosexuality was not legal in Britain until the passing of the 1967 Sexual Offences Act, which decriminalized sex in private between men over the age of twenty-one.
44. B. Theunissen, 'Closing the Door on Hugo de Vries's Mendelism': 248.
45. Morgan, 1909. Quoted in G. Allen, *Life Science in the Twentieth Century* (Cambridge University Press, 1978): 53–4.

Chapter 6: *Drosophila melanogaster*: Bananas, bottles and Bolsheviks

My main source for the **history of Drosophila** is Robert Kohler's work, particularly: 'Systems of production: Drosophila, neurospora, and biochemical genetics', *Historical Studies in the*

Physical and Biological Sciences, 1991: 87–130; and *Lords of the Fly: Drosophila Genetics and the Experimental Life* (University of Chicago Press, 1994). Garland Allen's work on Thomas Hunt Morgan and his career was also invaluable. Other sources included: E.A. Carlson, 'The 'Drosophila' group: The transition from Mendelian unit to individual gene', *Journal of the History of Biology*, 1974: 31–48; N. Roll-Hansen, 'Drosophila Genetics: A Reductionist Research Program', *Journal of the History of Biology*, 1978: 159–210; and S.G. Brush, 'How Theories became Knowledge: Morgan's Chromosome Theory of Heredity in America and Britain', *Journal of the History of Biology*, 2002: 471–535.

For the **Soviet Drosophila work and Chetverikov**, I have relied on Mark Adams's work, in particular: 'The Founding of Population Genetics: Contributions of the Chetverikov School 1924–1934', *Journal of the History of Biology*, 1968: 23–39; 'Towards a Synthesis: Population Concepts in Russian Evolutionary Thought', *Journal of the History of Biology*, 1970: 107–29; and 'Sergei Chetverikov, the Kol'tsov Institute, and the Evolutionary Synthesis', in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Harvard University Press, 1998). I also used: S.S. Chetverikov, *On Certain Aspects of the Evolutionary Process from the Standpoint of Modern Genetics* (1926; Genetics Heritage Press, 1997); T. Dobzhansky, 'The Birth of the Genetic Theory of Evolution in the Soviet Union in the 1920s', in *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, (Harvard University Press, 1998).

My thinking about this chapter and **experimental organisms in general** was greatly influenced by reading B.T. Clause, 'The Wistar Rat as a Right Choice: Establishing Mammalian Standards and the Ideal of a Standardized Animal', *Journal of the History of Biology*, 1993: 329–49.

For **chromosomes and classical genetics**, see: G.P. Rédei, *Genetics* (Macmillan, 1982); E.W. Crow and J.F. Crow, 'Walter Sutton and the Chromosome Theory of Heredity', *Genetics*, 2002: 1–4; S.R. Nelson and P.S. Nelson, 'Walter Sutton's chromosome theory of heredity: one hundred years later' (2002,

http://www.kumc.edu/research/medicine/anatomy/sutton/index.html); and O.S. Harman, 'Cyril Dean Darlington: the man who "invented" the chromosome', *Nature Reviews: Genetics*, 2005: 79–85.

Background material on **twentieth-century history, including eugenics**, came from: N. Stepan, *The Idea of Race in Science: Great Britain 1800–1960* (Macmillan, 1982); D.J. Kevles, *In the Name of Eugenics: Genetics and the uses of Human Heredity* (Penguin Books, 1986); W.H. Tucker, *The Science and Politics of Racial Research* (University of Illinois Press, 1994); and S.J. Gould, *The Mismeasure of Man* (Penguin Books, 1997).

The **banana details** are drawn from: N.W. Simmonds, *The evolution of the bananas* (Longmans, 1962); N.S. Price, 'The origin and development of banana and plantain cultivation', in *Bananas and Plantains* (Chapman & Hall, 1995); and V.S. Jenkins, *Bananas: an American history* (Smithsonian Institution Press, 2000).

Notes

1. C. Darwin to J. D. Hooker, [15 December 1876]: unpublished Darwin letter, Cambridge University Archives, DAR 95: 429.
2. Aristotle, *The History of Animals*, Book V: 19.
3. A.H. Sturtevant, *A History of Genetics* (1965; Cold Spring Harbor Laboratory Press / Electronic Scholarly Publishing Project, 2001): 43.
4. Kirby and Spence, *Introduction to entomology or elements of the natural history of insects* (1815).
5. [R. Chambers], *Vestiges of the Natural History of Creation: and other evolutionary writings* (1844; University of Chicago Press, 1994): 183.
6. J.A. Secord, *Victorian Sensation: The Extraordinary Publication, Reception, and Secret Authorship of Vestiges of the Natural History of Creation* (University of Chicago Press, 2000); J.A. Secord, 'Extraordinary experiment: Electricity and the creation of life in Victorian England', in *The uses of experiment: studies in the natural sciences* (Cambridge University Press); J.E. Strick,

Sparks of Life: Darwinism and the Victorian Debates over Spontaneous Generation (Harvard University Press, 2000).

7. A. Carnegie, *The Gospel of Wealth* (1900), quoted: in D.R. Oldroyd, *Darwinian Impacts: an introduction to the Darwinian Revolution* (University of New South Wales Press, 1980): 215.
8. William Graham Sumner, quoted in D.R. Oldroyd, *Darwinian Impacts: an introduction to the Darwinian Revolution*: 214.
9. Lord Roseberry, quoted in D. Trotter, 'Modernism and Empire: Reading The Waste Land', in *Futures for English* (Manchester University Press): 143–153: 150.
10. K. Pearson, *The Groundwork of Eugenics* (1909), quoted in W.H. Tucker, *The Science and Politics of Racial Research* (University of Illinois Press, 1994): 59.
11. Quoted in R.E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (University of Chicago Press, 1994): 26.
12. Fernandus Payne to A.H. Sturtevant, [16 October 1947]. Sturtevant Papers. Quoted in G.E. Allen, 'The introduction of *Drosophila* into the study of heredity and evolution, 1900–1910', *Isis*, 1975: 322–33: 330.
13. R.E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life*: 33–4.
14. W.S. Sutton, 'On the morphology of the chromosome group in *Bracystola magna*', *Biological Bulletin* 1902, 4: 24–39, and W.S. Sutton, 'The chromosomes in heredity', *Biological Bulletin*, 1903, 4,: 231–51. See E.W. Crow and J.F. Crow, 'Walter Sutton and the Chromosome Theory of Heredity', *Genetics*, 2002: 1–4: 1.
15. Morgan, *Evolution and Adaptation*, (London: Macmillan and Co. 1903): 286–287. Quoted in G.E. Allen, *Thomas Hunt Morgan: the man and his science* (Princeton University Press, 1978): 111.
16. X-rays were originally known as Röntgen rays in honour of their German discoverer, Wilhelm Conrad Röntgen.
17. G.E. Allen, *Thomas Hunt Morgan: the man and his science*: 152–3. Lilian Morgan's recollection was that it was *white* that

Morgan discussed so enthusiastically when their first child was born on 5 January 1910, but as Kohler has pointed out, she must have been mistaken: it could only have been *with* Morgan was talking about, as *white* did not turn up until May. R.E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life*: 46.

18. F.W. Taylor, *The Principles of Scientific Management* (1911; Routledge/Thoemmes, 1993).
19. Quoted in B.T. Clause, 'The Wistar Rat as a Right Choice: Establishing Mammalian Standards and the Ideal of a Standardized Animal', *Journal of the History of Biology*, 1993: 329–49: 343.
20. T.H. Morgan, 'Random Segregation Versus Coupling in Mendelian Inheritance', *Science*, 1911: 384; G.E. Allen, *Thomas Hunt Morgan: the man and his science*: 160–1.
21. By J.B.S. Haldane, see: R.E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life*: 47–8, 79–80.
22. G.E. Allen, *Thomas Hunt Morgan: the man and his science*: 191.
23. M.B. Adams, 'Sergei Chetverikov, the Kol'tsov Institute, and the Evolutionary Synthesis', in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Harvard University Press): 262–4.
24. T.H. Morgan to H. de Vries, [5 January 1918]. Archives of the Biological Laboratory, Vrije Universsiteit, Netherlands. My thanks to Elliot Meyerowitz for showing me this letter and to Tom Gerats for permission to quote from it.
25. R.J. Greenspan, *Fly Pushing: The theory and practice of Drosophila genetics* (Cold Spring Harbor Press, 1997): 125.
26. T.H. Morgan, 'A critique of the theory of evolution', Princeton; Princeton University Press, 1916.

Chapter 7: *Cavia porcellus*: Mathematical guinea pigs

The **primary sources** were: C.É. Brown-Séquard, 'Hereditary Transmission of an Epileptiform Affection Accidentally