

The Mysterious Origin of the Sweet Apple

On its way to a grocery counter near you, this delicious fruit traversed continents and mastered coevolution

Barrie E. Juniper

Apples! You can find more than a dozen varieties in the fruit section of your local grocery, or spread out in a stall by a farm gate on a back road—maybe even in your own yard in autumn. You'll likely know the names of your favorites: Jonathan, McIntosh, Red Delicious. If you live in Western Europe the selection might include Belle de Boskoop, Cox's Orange Pippin, Golden Delicious, Holstein or Ribston Pippin. Abundant apples ready for the eating can likewise be found in Eastern Europe and on through Asia to the Chinese border and the Gobi desert. You can grow this delicious fruit, with its very high levels of vitamins and valuable antioxidants, in your own back lot in almost any soil; you can store it in the cellar throughout the harshest of winters, and it will retain its flavor and value into the early spring. You may cook it, dry it or ferment it as you choose, but it is one of the very few food sources that you can pick, ripe from the tree, and eat without any preparation, peeling, grinding, hulling or other manipulation.

But what *is* this valuable and versatile fruit, and where did it come from? Is it the product, like so many plants, of the hybridization of numerous parents from distant lands? (Wheat has at least three parents, strawberries two

and roses no fewer than fourteen.) Does it have relations in the wild crab apples of North America such as the garland tree (*Malus coronaria*) or in Europe in the wild crab (*Malus sylvestris*)? Does it owe its size to some gross chromosomal change like polyploidization or a splitting or loss of existing chromosomes? Was it a chance discovery, like the kiwifruit, from a source of nutritionally relatively indifferent wild plants? The answer in every case above is *no*, but the truth is perhaps even stranger.

Remarkably, the parentage of every single one of the apple varieties listed above is unknown. Red Delicious emerged by chance in an Iowa fence row. It was spotted in about 1870 and bulked up by the Stark Nursery Company. Golden Delicious (no relation except that it's an apple) emerged as a chance seedling, in about 1890, in a hedgerow in West Virginia. It gained a particular claim to fame by being cloned into millions of grafted young trees by the officers of the Marshall Plan, and exported, after 1945, to revive the fruit industry of Western Europe.

It seems that many of our favorite apples have arisen by sheer chance. So what is the arithmetic basis of this lottery? The secret to the apple's origin lies in the fact that apple trees cannot normally pollinate themselves. Unlike, say, peaches, which can and do self-pollinate, predictably producing peaches virtually identical to the parents, the viable seeds (or pips) will produce apples, some of which may have value—but none of which will resemble the parents. Imagine the evolutionary power of the multiplicity of potential crosses in planted or wild orchards. Then multiply this potential by the fact that a range of bee species may act as pollen

vectors and that a female bee can forage for up to three kilometers.

Little wonder that there may be, throughout the temperate world, perhaps 20,000 distinct named apple varieties. There are, by contrast, only two varieties of commercial banana and just one of the kiwifruit. Moreover, with almost no exceptions, every single apple pip has the potential to grow into a new apple tree—there are virtually no sterile apples. Elite apples from this genetic kaleidoscope may be grafted to preserve their exact genetic character, but this is not essential. Apple trees on their own roots are perfectly viable. On the other hand, very many other commercial fruit crops, such as navel oranges and commercial bananas, are totally sterile and rely, eternally, for their genetic future and spread, on grafting or some other form of clonal propagation.

The Geological Framework

Long ago, probably some time between the end of the Cretaceous and the early Tertiary period (about 65 to 50 million years ago), the ancestors of the apple

Figure 1. Apples are so ubiquitous that we may be tempted to take them for granted. Yet their diversity and broad geographic distribution actually pose fascinating scientific questions. Why are there perhaps 20,000 varieties of apples but only two commercial varieties of bananas and one of kiwifruit? Is the sweet apple related to the so-called crabs? Were currently important commercial varieties—Red and Golden Delicious, for example—developed by hybridization or chromosomal changes? For that matter, where in the world did the apple come from? The author's probe of these and other mysteries of the apple's origins takes us to a remote mountain range in central Asia and introduces us to powerful evolutionary drivers such as the bear and horse. (Photograph courtesy of Keith Weller/USDA Agricultural Research Service.)

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Figure 2. Ancestors of the sweet apple probably crossed a land bridge between North America and Asia, settling into central China near what is now the city of Xi'an. A few million years ago, these neo-apples made their way westward into the Tian Shan range. Red lines are trade routes along which the apple later spread.

migrated west across the land bridge connecting what is now North America with Asia. Although the Bering Strait is currently a shallow sea with many islands, during at least 12 periods in the immediate geological past, seawater was locked in glaciers and ice sheets, and the two continents were connected by an ice-free bridge. Plants and animals would have moved, in both directions, through "Beringia" to their present locations. This little neo-apple would probably have looked more like a hawthorn (*Crataegus*) with bunches of long-stalked fruits not much bigger than peas. But by about 10 million to 12 million years ago there must have existed somewhere in what is now cen-

tral China, roughly in the area of the current provinces of Xi'an and Shaanxi, and perhaps in a great corridor of Tertiary temperate forest, a recognizable ancestral apple.

Much earlier, about 40 million years ago, the Indian subcontinent, which had detached from East Africa, crashed into the great northern land mass. Just like something pushing gently on the edge of a carpet, this thrust successively drove up the Himalayas, the Pamirs and the Tian Shan. India is still moving northward at several centimeters a year, as the mountain peoples of northwest India, Kashmir, Afghanistan and Tajikistan know full well. The Tian Shan, the last of the ripples as it were, began

to emerge as a distinct geological feature about 12 million years ago, and it is still lengthening and rising. In places, in those "heavenly mountains" (that is the translation), if you stand in one place, you may be 1.5 centimeters higher at the end of the year than you were at the beginning. The Tian Shan has by now lifted its peaks well above the snow line and lies as a great mountain range about 1,600 kilometers long and 640 kilometers in depth, running from what is now China in the east to Uzbekistan in the west. The east-west orientation, with about 20 parallel ridges, is important to our story.

The vast mass of the Indian Ocean to the south, through the constant warm monsoons, has kept the region ice free. The warming influence of these monsoons, in due season, can be detected deep into China. Unlike the continental regions of northern Europe and North America, the whole of the Tian Shan and regions to the south have not, at least in the immediate geological past, suffered glaciation. Large continental areas, as anybody who has spent a night in the desert will testify, lose heat very rapidly. Thus northern Europe and North America chilled out rapidly along the advance of the ice fronts, as, time after time, the glaciers moved deep to the south.

As a result of its "defense" by the warm Indian Ocean over millions of years, the Tian Shan has become a refuge for the sustained evolution of plants and animals. Almost no other area in the world has remained inviolate for so long. In contrast, most of North America and the British Isles and much of Western Europe were scraped clean by ice little more than 10,000 years ago. The spiky, permanently snow-covered peaks of the Tian Shan bear testimony to their ever-rising altitude and lack of glacial scraping. The mountains are constantly exposing new geological facies, disturbing existing drainage systems, wrecking existing patterns of vegetation and yet at the same time exposing fresh soil sites for exploitation by incoming seedlings. There is no geological peace in this fault-riven zone, from the Indian border to the edges of the great steppe lands of Kazakhstan.

Into this geologically restless but fecund environment moved, principally from the east, the ancestors of thousands of present-day plants, including those of many important crops and,



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Figure 3. The Tian Shan is the most recent mountain range to emerge from the collision of India with Asia. Currently rising at about 1.5 centimeters per year, the Tian Shan has never experienced glaciation. Snow-covered peaks provide abundant moisture to fruit forests in the valleys.

alongside them, many animals including bear, deer and wild pig. In the forest with these neo-apples would have developed apricots (*Prunus armeniaca*), pears (*Pyrus* spp.), pomegranates (*Punica granatum*), figs (*Ficus*), cherries (*Prunus avium* and *cerasus*) and the mulberries (*Morus*). To the west and south this new, mixed “fruit forest” would have been augmented by the walnut (*Juglans regia*).

Among the vegetation colonizing the Tian Shan came, likely via birds from the east, the ancestors of what we know as the “sweet” apple. The fruit probably then looked like a tiny, long-stalked, bitter apple something like *Malus baccata*, the Siberian crab. The pips may have been carried in a bird’s crop or clotted onto feet or feathers. A carrier-bird candidate is the beautiful azure-winged magpie (*Cyanopica cyanus*), which now occurs as relict but virtually identical populations at both ends of the transcontinental forest in southern Europe and eastern China.

It is, of course, impossible precisely to date this invasion, but we can be sure that the major players, both plant and animal, had found a place in the rising Tian Shan some time in the Mio-

cene Epoch of the Tertiary, at least 5.3 million years ago.

Given this geological turmoil, it should be no surprise that the individual species of the fruit forest are not long-lived trees; 30 years produces a fully productive apple specimen, and 100 years is about the maximum age that an apple, pear or apricot tree could normally be expected to survive. There is no premium on evolving, say, the longevity of a bristle-cone pine when your habitat is likely to disappear under an enormous rockfall or outwash fan well within a hundred years.

The Evolutionary Scene

From a neo-apple the size of a small grape, as we suppose the first colonizers to be, we now have, on our market shelves or in our gardens, a sweet apple the size of a tennis ball or even a softball.

Left behind, in both the evolutionary and geographical sense, is the spectrum of other apple species, sometimes crudely known as “crabs” and perhaps as many as 30 distinct species. These wild species are found principally in Central China (see Figure 8), but with substantial numbers in North



Figure 4. On arrival in the Tian Shan, the neo-apple likely resembled the tiny, long-stalked, bitter apple *Malus baccata*, the Siberian crab. (Illustration courtesy of Rosemary Wise.)

America and a few in Europe. These crabs (Saxon for bitter or sour), as they are sometimes derogatorily defined, are often of considerable decorative value—some have indeed played a

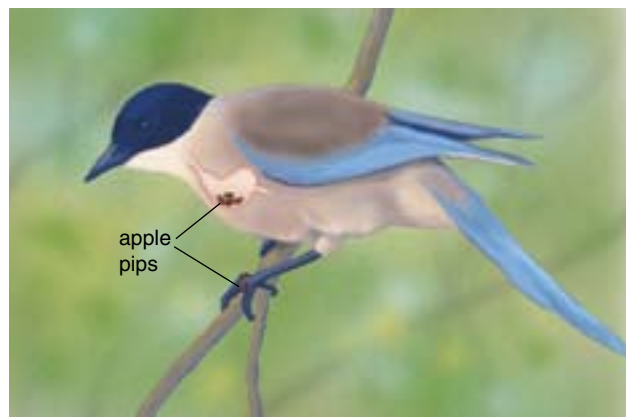
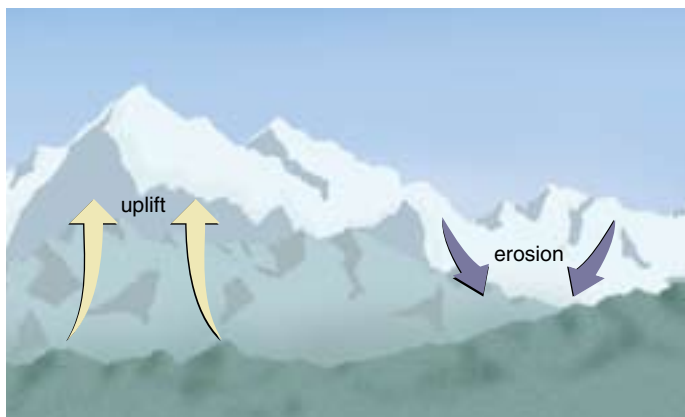


Figure 5. Forces driving the evolution of the sweet apple include the rapid uplift and erosion of the Tian Shan, producing fertile soils watered by melting snows (upper left). Into this rich environment, transported most likely by birds, came apple pips from central China (upper right). Indeed, the forests that developed in the valleys of the Tian Shan are rightly called fruit forests because of their abundant fruit-tree species. Along with the fruit came bears, who found the caves in the mountainsides and the forests below a welcoming habitat (left). Because smaller apples pass through bears (and to a lesser extent, wild horses) without dissolving the placenta, the pips of smaller apples were unable to fertilize, selecting for larger varieties.

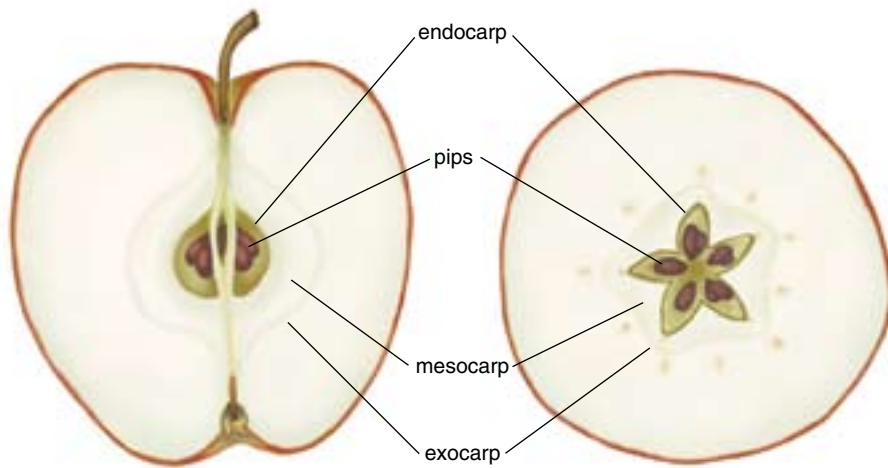


Figure 6. Apple anatomy, shown in longitudinal and latitudinal cross sections, features a central placenta that contains the pips, along with inhibitory agents that prevent the pips from germinating *in situ*. Only when the placenta is broken and the pips dispersed do apple seedlings emerge.

part in ornamental plant breeding—but the fruits are sour, sometimes even intolerably bitter and astringent. Thus they are of scant culinary value and, as we shall see later, seem to have contributed little if anything to the gene pool of the sweet apple.

What natural features of the unique Tian Shan might have contributed to this rigorous selection program? Time

is, as we have seen, not a problem. The turnover of individual trees is likewise conducive to the rapid evolution of a tree species, as is the fact that sweet apples are now, at least for all practical purposes, self-incompatible—that is, they cannot pollinate themselves. Therefore each apple tree within the forest and even each pip, usually five, within each individual fruit will be different. There are many apples on a mature tree, so natural selection has a rich and diverse population upon which to work.

Birds, of course, eat all manner of fruit. But most birds eat seeds—a dietary feature not conducive either to the selection or spread of a fruit tree. Sweet apples are often eviscerated by birds, but the seeds are frequently left in the empty shell of the pome. The reason is that apple (and pear and quince) seeds are rich in cyanoglycosides, which are highly repellent, particularly to birds. If you wish, you can smell a whiff of cyanide as you crunch two or three seeds between your teeth, but you would need a cupful of seeds to do yourself any harm! Moreover the placenta of the apple fruit, the womb, contains inhibitory substances that prevent the germination of the apple seed *in situ*. This is a commonly observed phenomenon in fruits as Michael Evenari showed in 1949. So what then does, or did, distribute the original apple seed?

The Engines of Evolution

The bear. Through the Miocene it would seem that brown bears (*Ursus arctos*)

migrated into the Tian Shan. As the mountain ranges began to rise, the nature of the geology would have provided an Elysium for bears and other forest-dwelling animals. To the east, beyond the Gobi desert where practically nothing can live, the flat loess-coated lands of China may be suitable for agriculture but provided no suitable habitat for cave dwellers. The unglaciated slopes below the Tian Shan ice pack are a perfect habitat, particularly where caves are washed out of the softer rocks by the constant flow of meltwater. A slice through a section of the Tian Shan would reveal cavities like the inside of a Gruyère or Emmentaler cheese.

Tian Shan bears have an impressively catholic diet—from wild rhubarb in the spring, through bee grubs and honey in the late summer to apples in the fall. Those long, rake-like claws not only serve to catch fish, dig for roots or tear open bee nests, which are abundant in the Tian Shan, but they also serve as garden rakes to harvest large or small fruit in quantity. North American black and brown bears (*Ursus americanus* and *Ursus arctos*) consume large quantities of fruits of all kinds in the fall, selecting the larger fruits or larger clusters. If we re-interpret this selection pressure to another continent, noting that this activity not only enhances the bear's food intake but also unconsciously selects for larger and larger fruits or bunches, we can comprehend the observed increase in the size of the apple.

Over millions of years, millions of bears just prior to hibernation slowly and unconsciously selected the larger and sweeter fruits of the neo-apples. Bears do have a sweet tooth, as A. A. Milne noted in *Winnie the Pooh*. The relative inefficiency of a bear's jaw in crushing fruit has another unintended consequence. As we have seen above, seeds that remain within the tissue (placenta) of the apple do not germinate. Herb Aldwinckle of Cornell University told me he has noticed that very small apples pass intact and uncrushed through a bear's jaws and gut and, in one or two cases, were seen intact in the fecal mass. The seeds in the small intact fruits would not have germinated. It does not pay, in a genetic sense, to be a very small apple in the Tian Shan. Compared to their counterparts of the North American continent, the bears (and the apple trees) and other inhabitants of the Tian Shan would have had 1,000 times as



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Figure 7. *Ursus arctos arctos*, the Eurasian or European brown bear, was likely the driving force behind the development of *Malus pumila*, the sweet apple. Its long claws are well adapted to gathering fallen fruit, and the catholic diet of all brown bears is well established.

long to indulge in some sort of mutual selection pressure. Wherever they are, bears learn quickly. The brown bears of Montana are known, as the artist Janet McGahan saw in 2001, to seek out and feed on the sweeter fruits of the grafted apple trees (imported *Malus pumila*) in planted orchards.

The jaws and guts of a bear, as Anna Traveset at the Mediterranean Institute for Advanced Studies and her co-workers have shown, do little or no damage to the teardrop-shaped, hard and tannin-coated apple pip. Traveset's group examined a wide range of gut-transmitted seeds, and in virtually every case the viability of the seeds was either neutral or enhanced. The fecal loads are dumped all over the Tian Shan in the fall—in a fertile mix of nitrogen-rich compost and, we have demonstrated in trial plots, carrying bear-viable apple seed. Then we suppose that, as on every other continent in the world, a spectrum of hard-working dung beetles will disperse, in their various ways, the whole fecal mass along with its fellow-traveling seeds.

Thus, probably over the whole of the Tian Shan but particularly on the northern slopes where the summer's heat was less fierce, there emerged, over millennia, an extraordinarily large apple, often sweet-textured and invariably with a very short stalk. The German/Russian explorer Johann or Ivan Sievers in 1793 discovered this apple. But he died shortly after discovering both the apple and the fruit forests. It was not until 1830 that Carl Friedrich von Ledebour in his new *Flora Altaica* named this apple in honor of his late colleague Sievers—*Malus sieversii*. This name is widely found in the literature. But it has more recently been discovered that the same apple, one of many that had escaped to the West over the previous thousands of years, had been named by Philip Miller in the United Kingdom in 1768 as *Malus pumila*, and, by reason of priority, the name *M. pumila* must take precedence.

The wild horse. Wild horses, which likewise had migrated from North America over Beringia, would have developed a taste for the wild apples on the margins of the new fruit forests. Sándor Bökönyi of the Archaeological Institute of the Hungarian Academy of Sciences believes that a few truly wild horses may still survive in the vast plains of Kazakhstan. The horse's jaw and gut, like that of the bear, do no harm to an apple pip. Moreover

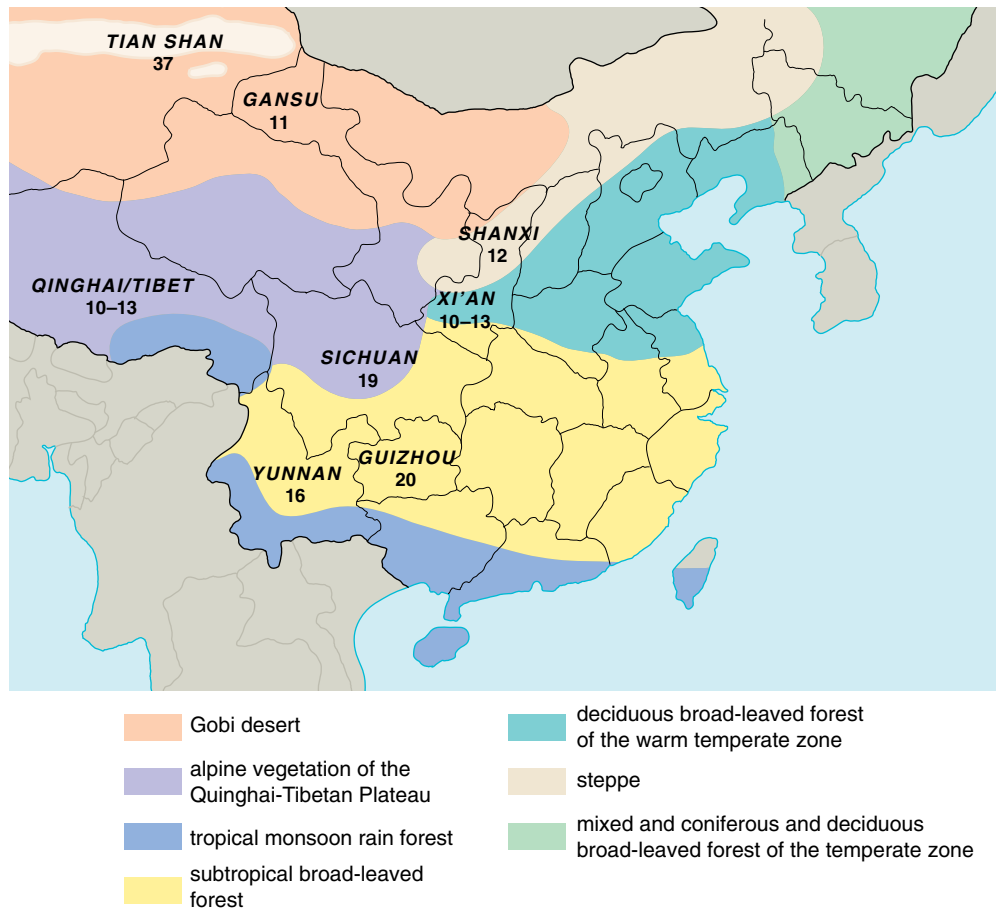


Figure 8. Areas of what was once forested central China are rich in *Malus*, with perhaps 37 distinct species. The numbers under the titles of provinces give an indication of this richness. On the other hand, the Tian Shan has only one dominant species, namely *Malus sieversii* or *M. pumila*, but the varietal richness of this species is almost infinite, far exceeding that of any other apple.

the horse probably would have ranged farther and more widely than the bear before dropping its fecal load.

But it is unlikely that the horse was a major engine for apple selection. Horses will not willingly penetrate into thick forest, and knowledge of the resident bears would have kept them wary. They may have browsed on the fruit but would have moved away to the safety of the open plains at night and commonly shed the seed upon stony ground. Nevertheless, long before their discovery by early humans they may also have moved to the grazing land around ancient oases, where their sharp hooves might have thrust seeds into the ground to establish new wild orchards. Wild horses may thus have contributed in a small way to the spread and diversification of the fruit components of the fruit forests and the mixing of the apple gene pool at least on the edges of the forest patches.

The domesticated horse. Once equines were in human employ, the whole scenario changed. The horse and the don-

key were domesticated, as elucidated by Carles Vila and his colleagues at Uppsala University, in what is now Kazakhstan some 7,000 years ago. In the guts of both horse and donkey, directed by human travelers, the apple pip moved west. The sharp hooves of these animals unwittingly planted the apple pips at every oasis. The east-west ridges of the Tian Shan, with rich valleys and their fortuitous patches of fruit forest between, would have determined the direction of the emerging trade routes. It is likely that these trade routes—later to be known as the “Silk Roads,” but actually in use long before silk was invented—began as animal-migration tracks leading from one oasis or rich grazing ground to another.

The Evidence from the DNA

But if the earliest travelers, with their newly domesticated horses or donkeys, began to travel westward from one oasis to another, is it not likely that the emerging sweet apple of the Tian Shan could have hybridized with other species of apples that lay in its path as

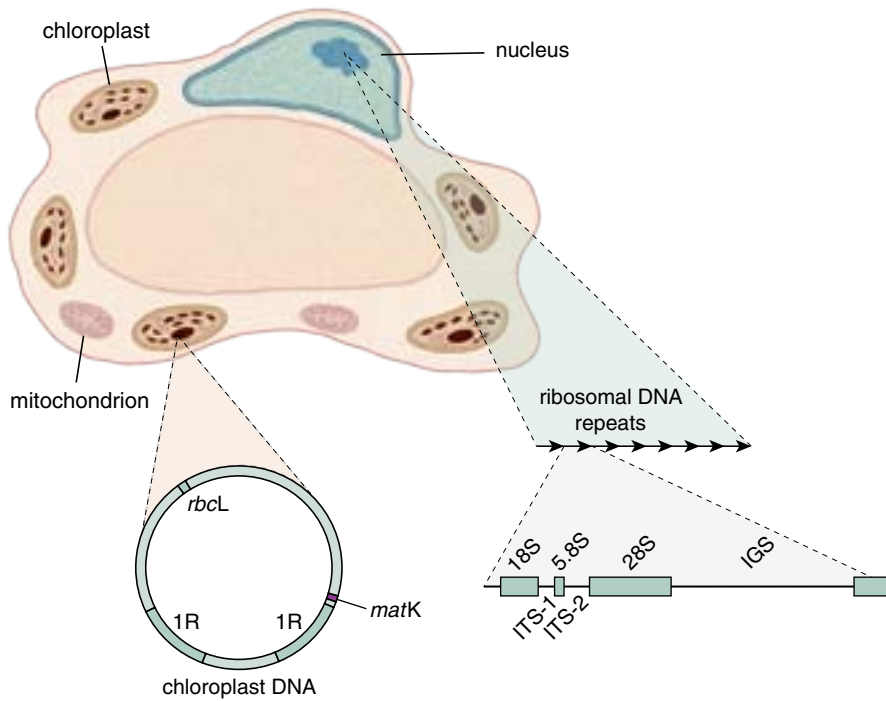


Figure 9. Two types of DNA prove useful in developing phylogenies of apple varieties. Chloroplast DNA can readily be extracted from chloroplasts, whereas nuclear DNA, including the ribosomal internal transcribed spacer gene (ITS), can be garnered from the cell nucleus.

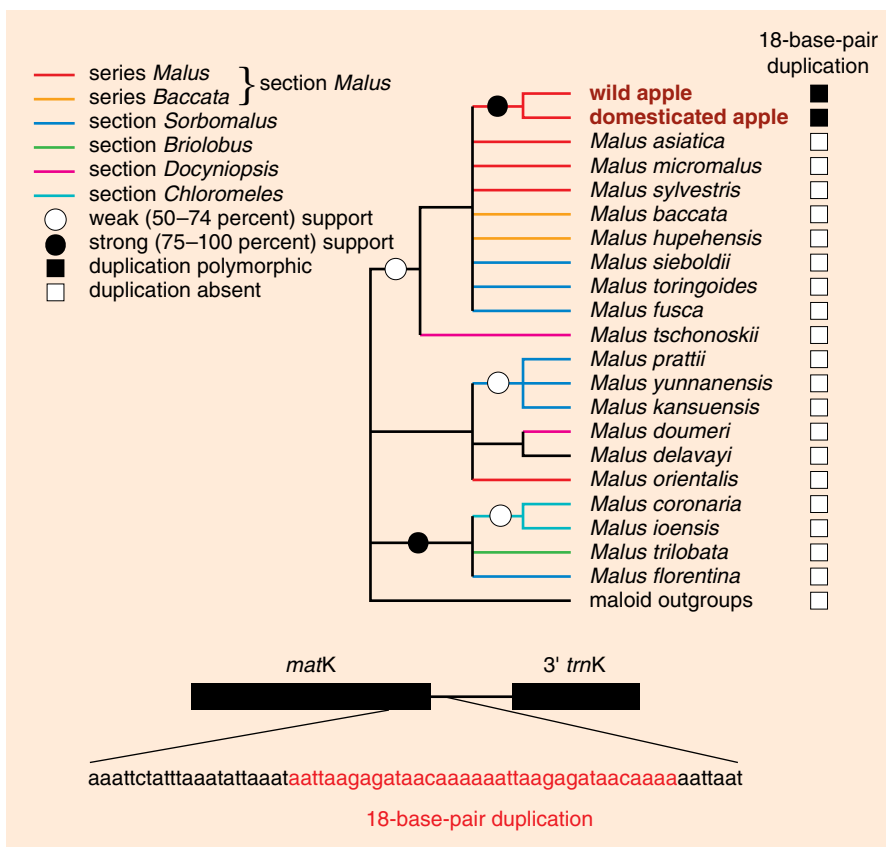


Figure 10. Phylogeny of the chloroplast-encoded gene *matK* shows two 18-base-pair duplications present only in Tian Shan wild apples and domesticated apples, pointing to the Tian Shan as the original source of *Malus pumila*. Apple taxonomy is quite complicated, owing in part to the thousands of varieties. Two additions to taxonomic hierarchy—section and series between genus and species—help distinguish these plants. In this and Figure 11 the circles refer to the degree of statistical support for groupings. (Adapted from Harris, Robinson and Juniper 2002.)

it traveled west? Sporadically within the Tian Shan can be found *Malus baccata*. In Khirgistan can be found *Malus khirgizorum*. As the apple, this welcome economic migrant, reached eastern Europe, it would have come within the range of *M. trilobata* in the Levant, with *M. florentina* in Italy and with *M. sylvestris* over most of the more northern lands of western Europe. Yet it does not seem, as Els Coart with the Agricultural Research Centre in Ghent and her colleagues discovered, that either by accident or by intent was there any significant gene flow between *M. pumila* and any other apple species. The timing of the flowering period of *M. pumila* is not dissimilar to any other apple species. The only feature unique to *M. pumila* among all species of *Malus* seems to be that it lacks, or virtually lacks, an endosperm. This might, as Liliana Costa and her colleagues here at Oxford have suggested, through epigenetic control, determine a choice of partners.

In plants, there are three sources of DNA within every cell, all of which can be used to detect relationships through their mutations. In this study both the nuclear and the chloroplast DNA have proved useful (see Figure 9). The chloroplast DNA provides data about the evolutionary relationships of the maternal line because chloroplasts in *Malus* and in most higher plants are transmitted to the next generation through the eggs. Any evidence of hybridity may be revealed by the nuclear DNA, and, fortunately, the DNA from *Malus* is readily extracted.

As Stephen A. Harris, Julian P. Robinson and I have shown, both the wild apple, represented through direct collections of material in the Tian Shan, and domesticated apples cluster closely together, as a phylogeny based on the ribosomal internal transcribed spacer (ITS) gene shows (Figure 11). Duplications in the *matK* gene (Figure 10) indicate that from very different locations in the Tian Shan, there were at least two separate importations of wild apples from the region—in all probability there were many more. The occurrence of these two shared 18-base-pair duplications and the absence of these duplications in *M. sylvestris*, often cited as a potential hybrid partner, show the close affinity of the wild Tian Shan apple with the sweet apple. Note too that the other European species *M. trilobata* and *M. florentina* lie far away

from any possible recent phylogenetic relationship. In the ITS diagram, *M. niedzwetzkyana* is considered now to be just a rare colored form of the wild apple and *M. orientalis* and *M. prunifolia* are no more than local variants of the wild apple.

Migration to the West

As horse transport developed along the east-west trade routes, this “new” apple, a welcome migrant, would have moved into areas that were already at a fairly high level of sophistication in agricultural terms. The Fergana Valley, now in Uzbekistan, was one of the first areas in the world where the pioneer techniques of agriculture, the Neolithic revolution, were practiced. The tracks would have led onward to higher, cooler lands—not, at first, into the steaming hot Tigris-Euphrates valley—on the northern edges of the great Persian empires. The new apple would have found both fertile ground and, in all likelihood, ready acceptance as a new fruit to add to the already well-established fig, date and vine.

It seems possible that grafting was invented in the Tigris-Euphrates valley, perhaps around Babylon, as irrigation and tropical heat raised the salinity of the soil. A combination of salt-tolerant stocks with indifferent grapes, was found to be able to support, on a graft, high-quality grapes with low salt tolerance. The technique would readily have been transferred to other top fruit, including apples, which were growing in the cooler, higher ground to the north. Both seedling and grafted apples began to move into Europe. From Europe the apple moved across the seven seas. And now, through its immense fecundity and diversity, the sweet apple, *Malus pumila*, is not only one of the major crops of the temperate zone, but seedling apples, sometimes of high quality, continue to emerge in hedgerow, ancient trackway or neglected gardens, defying both the grasp of agribusiness and the imposition of government diktat.

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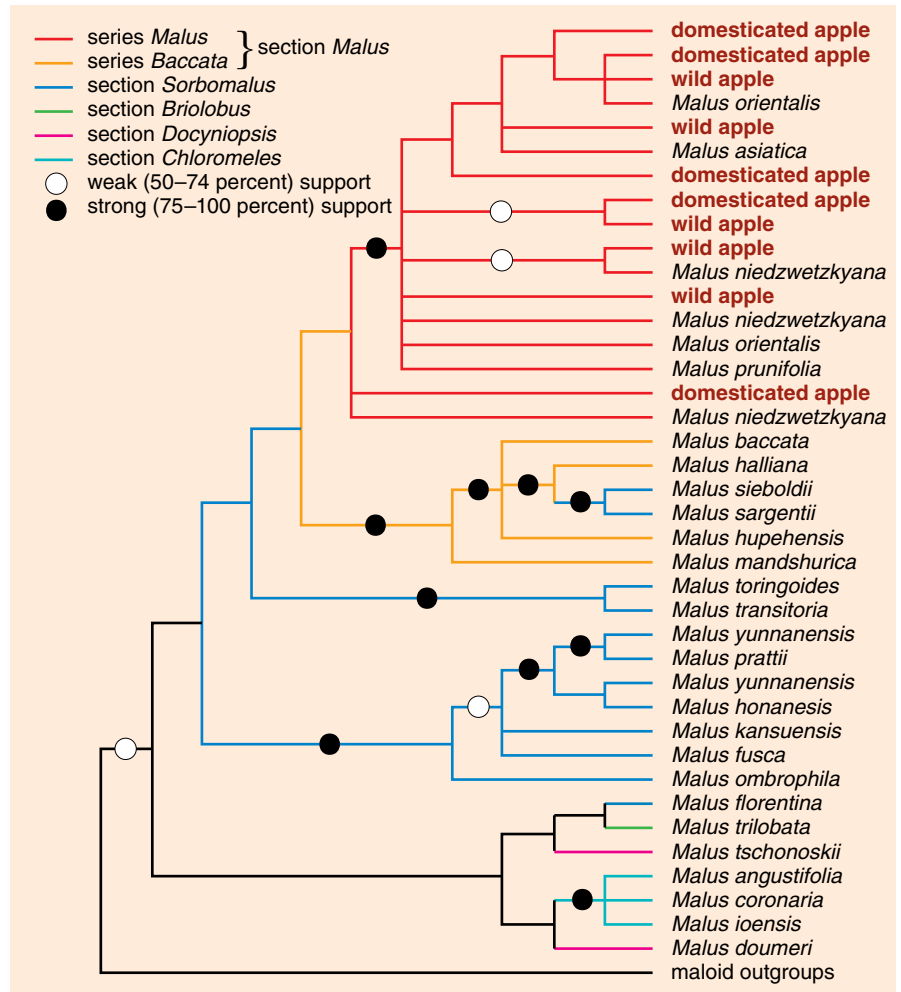


Figure 11. Phylogeny of the nuclear ribosome internal transcribed spacer (ITS) gene helps group various apple varieties. Further, these groupings show that wild apples (*Malus sieversii*) from central Asia are quite similar to domesticated apples, and that several other *Malus* species are nearly indistinguishable. (Adapted from Harris, Robinson and Juniper, 2002.)

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