

# The origin and evolution of a favorite fruit

The origin of strawberry is truly global, involving both natural processes and human intervention. The strawberry genome sequence provides support for an influential hypothesis of genome dominance.

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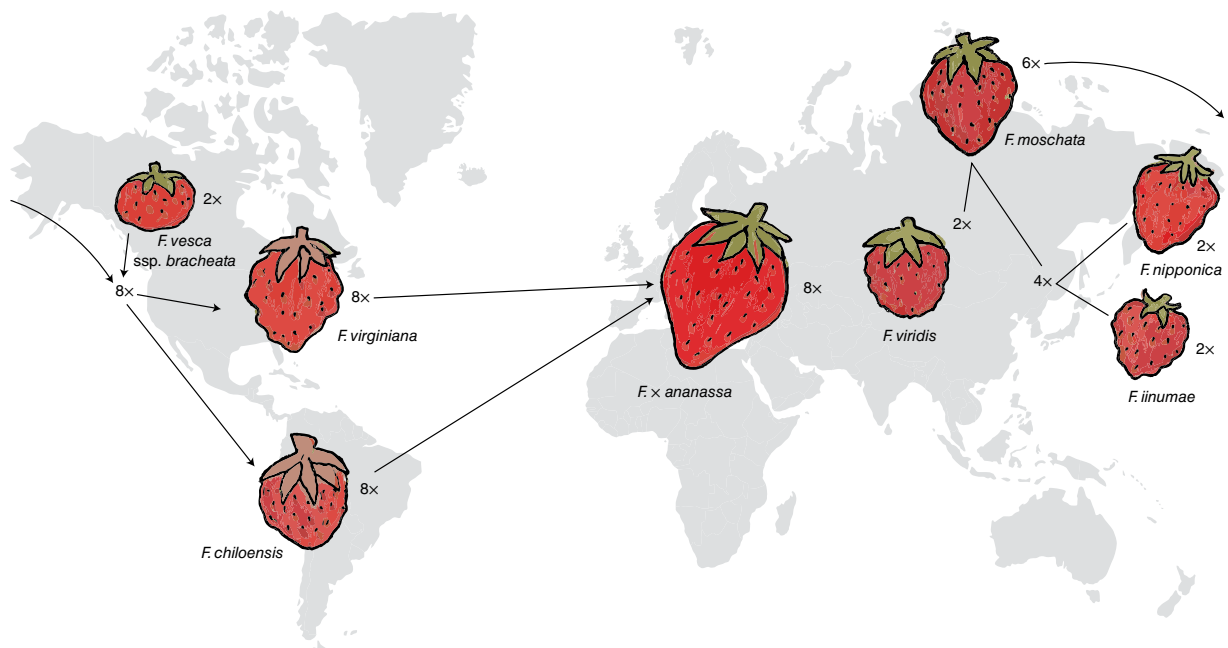
The succulent fruits and vegetables available in our greengrocers and supermarkets are markedly different from the wild foods that were foraged by our hunter-gatherer ancestors. At the same time as these plants have transformed our lives, and indeed human societies, the process of domestication has transformed the plants and created new species. In this issue, Edger and colleagues present a beautiful study on the origin and evolution of one of the world's favorite fruits, the strawberry<sup>1</sup>. The study reveals a complex history that spans both Old and New Worlds, and involves both natural processes and human intervention. Furthermore, the story is told in both geographic and genomic detail.

## Globe-trotting strawberries

The genus of strawberry, *Fragaria*, has many species. They bear small seeds that are easily

dispersed; consequently, the genus is native to both Old and New Worlds (even isolated Hawaii has a species). Furthermore, the species themselves are wide ranging and hybridize easily<sup>2</sup>. These hybridization events have formed polyploid species whose nuclei contain essentially complete chromosome sets from more than one species (with each chromosome set forming a 'subgenome'). The nuclei of diploid species (2 $\times$ ), with the basal number of chromosomes, contain seven pairs of chromosomes. Tetraploid species (4 $\times$ ) have 14 pairs, hexaploid species (6 $\times$ ) have 21 pairs, and octoploid species (8 $\times$ ) have 28 pairs. Fitting with the general trend in which polyploids are favored during domestication<sup>3</sup>, the modern cultivated strawberry, *Fragaria*  $\times$  *ananassa* has the highest of these ploidies. To clarify species relationships, Edger and colleagues<sup>1</sup> carried out a comprehensive phylogenetic analysis comparing the sequences of the expressed

genes of multiple accessions of all diploid species to the genome of *F.  $\times$  ananassa*. Their analyses identified all four diploid species ancestral to *F.  $\times$  ananassa*, thus providing strong support for two previously identified ancestors: a species endemic to Japan, *Fragaria iinumae*, and a species broadly distributed across the Northern hemisphere, *Fragaria vesca*. Furthermore, they were able to indicate that a particular subspecies, *F. vesca* ssp. *bracheata*, endemic to the western part of North America, was involved in the hybridizations. Most excitingly, they were able to provide the first identification of the two diploid species that donated the other two chromosome sets to *F.  $\times$  ananassa*: another species from Japan, *Fragaria nipponica*, and the Eurasian species *Fragaria viridis*. The hybridizations form a polyploid series spanning diploid, tetraploid, hexaploid and octoploid species, which are distributed across Eurasia and



**Fig. 1 | Schematic showing the hybridizations that gave rise to *Fragaria ananassa*.** Ploidies are indicated: diploid, 2 $\times$ ; tetraploid, 4 $\times$ ; hexaploid, 6 $\times$ ; and octoploid, 8 $\times$ . Species are placed on the world map according to their approximate geographical locations. Converging lines represent hybridizations, and arrows represent the movement of species. Publ. note: Springer Nature is neutral about jurisdictional claims in maps.

the Americas (Fig. 1). The octoploid stage has been estimated to have occurred more than 1 million years ago (ref. <sup>4</sup>). Evolutionary divergence of the ancestral octoploid gave rise to two present-day species, *Fragaria virginiana* and *Fragaria chiloensis*. The final hybridization was only approximately 300 years ago, courtesy of market gardeners in Europe. One of the octoploid species, *F. virginiana*, was being cultivated in Europe by the sixteenth century. Then, in the eighteenth century, a few specimens of the other octoploid species, *F. chiloensis*, were brought to France from Chile by an explorer, Amédée Frézier. However, he brought only female plants. Fortunately, cultivation in proximity to *F. virginiana* allowed for cross-pollination and development of fruit. Thus, the hybrid *F. × ananassa* was produced<sup>5</sup>. Its size, taste, fragrance and ease of cultivation have ensured its spread around the globe, its popularity and its improvement through breeding ever since.

#### Cohabitation and genome conflict

Polyploid plants have long seemed to be favored for cultivation and domestication<sup>3</sup>. Multiple subgenomes contained in a single nucleus have been postulated to essentially confer a fixed hybrid vigor. However, this nuclear cohabitation also generates stress and adaptation. Generally, the more divergent the genomes of the ancestral species, the more genomic conflict has been suggested to be generated. Genome conflict

often leads to one subgenome ‘dominating’ the other. The new genome sequence and gene expression data allowed Edger et al.<sup>1</sup> to test an influential ‘subgenome-dominance hypothesis’<sup>6</sup>. This hypothesis predicts that subgenomes with higher densities of transposable elements will, via the spillover of mechanisms that suppress their activity toward neighboring genes, generally have lower gene expression. Over generations, the loss of genes from subgenomes with lower gene expression will be favored over the loss of genes from subgenomes with higher gene expression. Loss of genes can occur through deletion or genetic recombination that replaces genes from one subgenome with corresponding genes from a different subgenome (homoeologous exchanges). The data reported by Edger et al.<sup>1</sup> neatly support this hypothesis. The authors identify that the genome of the last species to join in the polyploid series, *F. vesca*, contributed the dominant subgenome. Compared to subgenomes derived from the other ancestral species, the *F. vesca* subgenome has 20% fewer transposable elements and generally higher gene expression, and it has retained 20% more genes. The retained genes include tandemly repeated genes, such as nucleotide-binding-site leucine-rich repeat (NBS-LRR) genes, that are important in conferring resistance against plant pests and diseases. Furthermore, the analyses revealed that key metabolic pathways, including those that give rise to

the characteristic strawberry flavor, color and fragrance, are largely controlled by the dominant subgenome.

Because a genome sequence is a landmark for research on a crop’s biology, the genome sequence of octoploid strawberry is particularly welcomed. Beyond having already provided support for a key hypothesis of plant polyploid-genome evolution, the genome sequence will provide a catalog of gene content and a framework for molecular breeding and future research. □

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#### Competing interests

The authors declare no competing interests.