

On the origin of strawberries

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High-quality genomes of the cultivated strawberry's progenitors provide the strongest evidence to date for the identity and chromosomal composition of the four subgenomes of octoploid strawberry.

The origin of the cultivated strawberry *Fragaria* × *ananassa* from two wild species brought together in the famous strawberry growing region of Brest, France in the first decades of the eighteenth century is well-known (Fig. 1). In the 1760s, the French botanist Antoine Nicolas Duchesne elucidated the parentage and recreated the cultivated strawberry by crossing *Fragaria virginiana* and *F. chiloensis*¹. At the age of 19, he published his results in an expansive 460-page strawberry monograph. The evolutionary history of the two wild octoploid species, which, like the cultivated strawberry, have four subgenomes, has been an open question ever since Duchesne first proposed that the woodland strawberry *F. vesca* was their progenitor. High-quality genomes of *F. virginiana* and *F. chiloensis* are published in this issue of *Nature Plants*. Jin et al. provide compelling evidence for how to resolve the diploid ancestry and chromosomal composition of the four subgenomes of the octoploid strawberries².

The octoploid nature of *F. × ananassa* and its wild progenitors was discovered nearly 100 years ago by counting chromosomes^{3,4}, but the small size of strawberry chromosomes limited what could be inferred about their subgenome composition. Cytogenetic and early Sanger sequencing studies provided evidence for *F. vesca* as a contributor to the octoploid genome, but further progress was slow. It was not until 2009 that *F. iinumae* (restricted to Japan and Sakhalin Island) was identified as a second diploid progenitor on the basis of the phylogenetic analysis of two low-copy nuclear genes⁵. A further refinement published in 2012 was the use of chloroplast genome sequences to identify *F. vesca* subsp. *bracteata* (northwest North America) as the direct source of the A subgenome⁶.

The hypothesis that *F. iinumae* is also the closest living ancestor of the two remaining subgenomes was first proposed⁷ in 2014. Limitations of that study were the relatively small number (317–902) of informative markers per chromosome and the absence of an octoploid genome to validate the results. The landmark 2019 publication⁸ of the first chromosome-scale *F. × ananassa* 'Camarosa' genome confirmed the *F. vesca* and *F. iinumae* subgenomes but proposed that the remaining two subgenomes originated with the diploid species *F. nipponica* and *F. viridis*. While this four-species hypothesis has been widely cited, it has not been recovered in subsequent independent analyses of the *F. × ananassa* 'Camarosa' genome. Studies based on the phylogenetic

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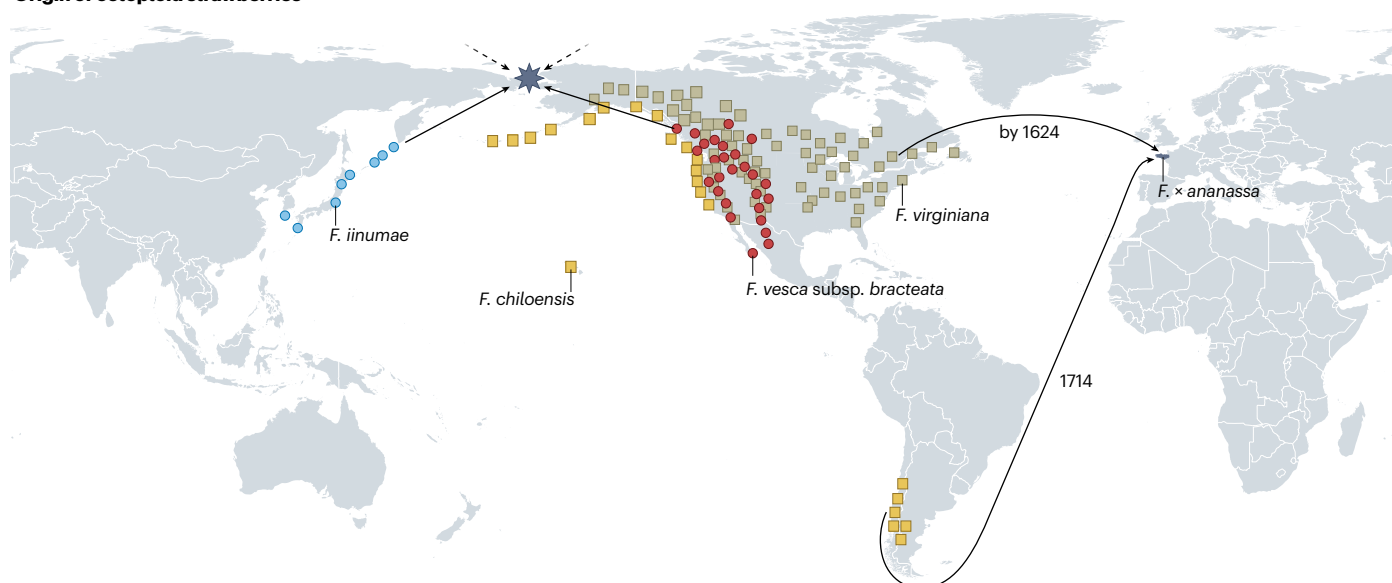


Fig. 1 | Map showing the ancient (~1.5 million years ago) hybrid origin of the octoploid strawberry (eight-pointed star, dashed arrows are presumed extinct), the recent (300 years ago) hybrid origin of the cultivated strawberry, and the natural distribution of the progenitor species (circles, diploid; squares, octoploid). Jin et al. provide strong support for an octoploid

origin involving *Fragaria vesca* subsp. *bracteata*, *F. iinumae*, and one or two presumed extinct species related to *F. iinumae*. Also shown are the locations where *F. chiloensis* and *F. virginiana* were collected and brought to France and the location of their hybridization in northern France (Brittany) to create the cultivated strawberry, *F. × ananassa*.

analysis of diploid genomes and octoploid subgenomes⁹, short read mapping¹⁰ and identification of subgenome-specific *k*-mers^{11,12} consistently resolve *F. iinumae* as the closest living relative to three of the four subgenomes.

Jin et al. combine all three of these approaches and present the first analyses to include both the *F. viridis* and *F. nipponica* genomes together with octoploid genome sequences outside *F. × ananassa* ‘Camarosa’. Their comprehensive analyses provide compelling evidence against *F. viridis* and *F. nipponica* ancestry of the octoploid strawberries. In addition, the clustering of subgenome-specific *k*-mers conducted here, and in two previous studies of *F. × ananassa* ‘Camarosa’^{11,12}, reassign three pairs of homeologous chromosomes between the C and D subgenomes. This represents an important advance in our understanding of the octoploid strawberry genome and will serve as a strong foundation for future comparative (sub)genomics.

What was the source of the evidence for *F. viridis* and *F. nipponica* ancestry? The original PhyDS algorithm required that each subgenome have a different diploid ancestor, since whenever multiple octoploid genes resolved as sister to the same diploid it was considered to be a case of ambiguous orthology⁹. This limitation was addressed with PhyDS v. 2.1 (ref. 13). However, the reanalysis only tabulated gene trees in which the C and D subgenomes are sister to *F. iinumae*, excluding the B subgenome¹⁴. Thus, the most common phylogenetic resolution, as presented by Jin et al., was not considered. In other words, the evaluated models of subgenome ancestry^{8,13} excluded what multiple independent analyses^{2,9–12} conclude is the most likely evolutionary history of octoploid ancestry.

How important is it to know the identity of the diploid ancestors of a polyploid? Plant breeders have long looked to crop wild relatives as critical sources of useful genetic variation. In the case of the cultivated strawberry, these results should encourage focused efforts to collect, preserve and characterize accessions of *F. vesca* subsp. *bracteata* and *F. iinumae*.

Several questions remain about the evolutionary details of the octoploid origin. Jin et al. describe the C and D subgenomes as “closely related yet still distinguishable”. The pattern of shared *k*-mers is consistent with an initial tetraploid combining these two subgenomes¹². Was this an autotetraploid or an allotetraploid? How long did it persist

as an independent lineage? The same *k*-mer evidence suggests the existence of a hexaploid comprising the B, C and D subgenomes. This hexaploid is estimated to have originated ~3 million years ago, while the octoploid originated ~1.5 million years ago¹². This late Neogene or early Pleistocene timing and current species distributions lead to the hypothesis that these polyploidy events occurred in Beringia (Fig. 1), which at that time was covered in mixed coniferous forests with a diverse herbaceous understory¹⁵. Advances in environmental DNA sequencing have recovered over 100 different plant genera from a 2-million-year-old ecosystem in northern Greenland¹⁶; perhaps in the future eDNA will confirm the presumed extinct diploid, tetraploid and hexaploid ancestors of the cultivated strawberry.

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References

1. Lee, V. in *The Strawberry — History, Breeding and Physiology* Ch. 3–5, 15–72 (Holt, Rinehart & Winston, 1966).
2. Jin, X. et al. *Nat. Plants* <https://doi.org/10.1038/s41477-023-01473-2> (2023).
3. Ichijima, K. *Genetics* **11**, 590–604 (1926).
4. Longley, A. J. *Agric. Res.* **32**, 559–568 (1926).
5. Rousseau-Gueutin, M. et al. *Mol. Phylogenet. Evol.* **51**, 515–530 (2009).
6. Njuguna, W., Liston, A., Cronn, R., Ashman, T.-L. & Bassil, N. *Mol. Phylogenet. Evol.* **66**, 17–29 (2013).
7. Tennessen, J. A., Govindarajulu, R., Ashman, T.-L. & Liston, A. *Genome Biol. Evol.* **6**, 3295–3313 (2014).
8. Edger, P. P. et al. *Nat. Genet.* **51**, 541–547 (2019).
9. Liston, A. et al. *Nat. Genet.* **52**, 2–4 (2020).
10. Feng, C. et al. *Mol. Biol. Evol.* **38**, 478–485 (2021).
11. Jia, K.-H. et al. *New Phytol.* **235**, 801–809 (2022).
12. Session, A. M. & Rokhsar, D. S. *Nat. Commun.* **14**, 3180 (2023).
13. Edger, P. P. et al. *Nat. Genet.* **52**, 5–7 (2020).
14. Liston, A. & Ashman, T.-L. *Acta Hort.* **1309**, 107–118 (2021).
15. Fletcher, T. L., Telka, A., Rybczynski, N. & Matthews, J. V. *Palaeontol. Electronica* **24**, 1–62 (2021).
16. Kjær, K. H. et al. *Nature* **612**, 283–291 (2022).

Competing interests

The author declares no competing interests.