New tomato, potato family tree shows that fruit color and size evolved together

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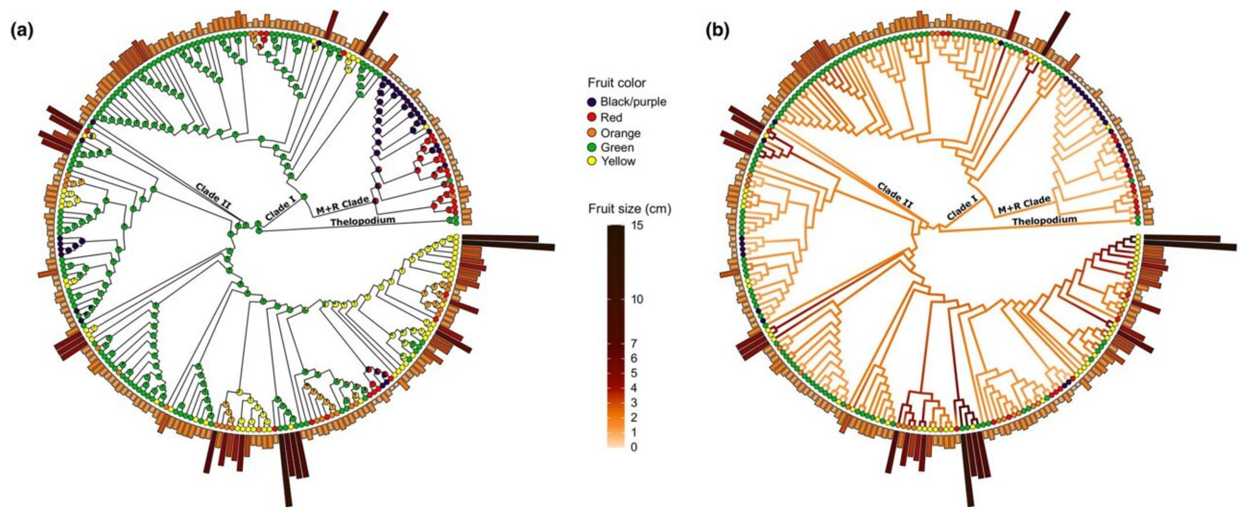

Circular phylogenetic trees of Solanum showing ripe fruit colors and size mapped onto terminal tips and ancestral character reconstructions at the internal nodes for color (a) and size (b). Credit: *New Phytologist* (2024). DOI: 10.1111/nph.19849

Fruits of Solanum plants, a group in the nightshade family, are incredibly diverse, ranging from sizable red tomatoes and purple eggplants to the poisonous green berries on potato plants. A new and improved family tree of this group, produced by an international team led by researchers at Penn State, helps explain the striking diversity of fruit colors and sizes and how they might have evolved.

The team found that the size and color of fruits evolved together and that fruit-eating animals were like not the primary drivers of the fruits' evolution, as had been previously thought. The study, published in the journal *New Phytologist*, may also provide insight into breeding agriculturally important plants with more desirable traits, the researchers said.

"There are about 1,300 species in the genus Solanum, making it one of the most diverse plant genera in the world," said João Vitor Messeder, graduate student in ecology and biology in the Penn State Eberly College of Science and Huck Institutes for the Life Sciences and lead author of the paper.

"Since the 1970s and '80s, researchers have suggested that birds, bats and other fruit-eating animals have driven the evolution of fruits like those in Solanum. However, the importance of the evolutionary history of the plants has been underestimated or rarely considered when evaluating the diversification of fleshy fruits.

"To better test this hypothesis, we needed first to produce a more robust phylogeny, or family tree, of this plant group to improve our understanding of the relationships between species."

Plants in the genus Solanum produce fruits with a wide variety of sizes, colors and nutritional values. They can appear black, purple, red, green, yellow or orange and range in size from less than a quarter of an inch to as much as 8 inches, or 0.5 to 20 centimeters.

In addition to agriculturally important plants, some plants in the group are cultivated for their ornamental flowers, and the fruits of many of these plants are eaten by humans and a large diversity of animals, including birds, bats, reptiles, primates and other land mammals.

The researchers collected samples of plants from across the world, including wild plants from Brazil, Peru and Puerto Rico and plants from botanical gardens, and sequenced their genes from RNA.

They supplemented with previously collected samples and publicly available data, ultimately comparing the sequences of 1,786 genes from a total of 247 species to reconstruct the Solanum family tree. This included representatives from all 10 of the major clades—the branches of the tree—and 39 of 47 minor clades within the genus.

"By using thousands of genes shared among species that effectively represented the entire genus, we significantly improved the Solanum family tree, making it the most comprehensive to date," said Messeder, who conducted the research in the lab of Hong Ma, Huck Chair in Plant Reproductive Development and Evolution and professor of biology at Penn State and a co-corresponding author of the paper.

"Recent advances in technology allowed us to use more genes than previous studies, which faced many challenges in resolving relationships between species and clades. This improved tree helps us understand when different fruit colors and sizes originated or how they changed as new plant species came about."

The researchers added considerable resolution of the smaller branches in the group that includes potatoes and tomatoes, as well as their closely and more distantly related wild species. The insights gained, the researchers said, could support crop improvement programs for these species and other crops in the genus.

"If the closest wild relatives of important agricultural crops have desirable traits, it is possible to breed crops with those species or borrow their genes, for example, to improve resistance to temperature or pests or to produce larger fruits or fruits of a certain color," Messeder said.

The researchers found that the color and size of Solanum fruits was fairly conserved over evolutionary history, meaning that closely related species tend to have similar fruits. The evolution of fruit color and size is also correlated, with changes in one trait often corresponding to changes in the other, leading fruits of certain colors to be bigger than fruits of other colors.

"These results suggest that physiological and molecular mechanisms may play a role in keeping the evolution of fruit color and size tied together," Messeder said. "While frugivores—or animals that primarily eat fruit—and seed dispersers may influence diversification, we need to consider all of the possibilities when studying how fruits became so diverse."

The researchers also clarified the origin and diversification timeline of this genus, in part by including recent information from the oldest nightshade family fossil—from a different genus in the Nightshade family whose fossil was dated to about 52 million years ago—and from particular genes that improved estimates of the length of evolutionary branches.

The researchers dated the origin of Solanum to about 53.1 million years ago—a full 30 million years earlier than prior estimates that were based on genes from other parts of the plant cell. This paints a new picture of the environment that might have shaped how these plants diversified into new groups and species.

"The Earth's environment changed dramatically during the 30 million years in terms of temperature, carbon dioxide in the atmosphere, geography and animal diversity," Messeder said. "Now that we know when Solanum and its subgroups originated, we can think about the conditions that might have promoted the diversification of that group, as well as how other organisms might have played a role."

The team found that the earliest members of Solanum had medium-sized berries that remained green when ripe, and that green and yellow fruits of this group became more diverse around 14 million years ago.

The researchers speculated that bats might have played a role in this diversification, given their similar evolutionary timeline and that they are the primary dispersers of modern green and yellow Solanum fruits. As new bat species arose and expanded where they were living during this time, they ate Solanum fruits and carried their seeds to new environments.

Next, the researchers plan to explore how modern interactions between animals and the fruit they eat may shed light on the evolution of both groups as well as explore the evolution of certain genes relevant to fruit color and size.

More information: João Vitor S. Messeder et al, A highly resolved nuclear phylogeny uncovers strong phylogenetic conservatism and correlated evolution of fruit color and size in Solanum L., *New Phytologist* (2024). DOI: 10.1111/nph.19849

Provided by Pennsylvania State University

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