Hail to the Hornworts: New Plant Family Tree Sheds Light on Evolution of Life Cycles

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In the history of life on earth, one intriguing mystery is how plants made the transition from water to land and then went on to diversify into the array of vegetation we see today, from simple mosses and liverworts to towering redwoods.

A research team led by University of Michigan evolutionary biologist Yin-Long Qiu has new findings that help resolve long-debated questions about the origin and evolution of land plants. The work will be published online this week in the *Proceedings of the National Academy of Sciences*.

Two major steps kicked off the chain of events that helped land plants prosper, forming the basis for modern land-based ecosystems and fundamentally altering the course of evolution of life on earth, said Qiu. The first step was the colonization of land by descendents of aquatic plants known as charophyte algae. That event opened up a vast new world where the sun's intensity was undiminished by passage through water and where carbon dioxide---another essential ingredient for plant life---was abundant.

The second event was a key change in plant life cycles. Plants exhibit a phenomenon known as alternation of generations, in which two alternating forms with different amounts of DNA make up a complete life cycle. One form, known as a sporophyte, produces spores, which grow into individuals of the other form, called gametophytes. Gametophytes produce gametes---eggs and sperm---which unite to form a fertilized egg capable of becoming a new sporophyte, thus completing a life cycle. While all plants exhibit alternation of generations, some spend most of their life cycle as sporophytes, and others spend more time in the gametophyte phase.

"Early in the history of plant evolution, a shift occurred," said Qiu, assistant professor of ecology and evolutionary biology. "If you look at the so-called 'lower' plants such as algae, liverworts and mosses, they spend most of their life cycle as gametophytes. But if you look at plants like ferns, pines and flowering plants, they spend most of their time as sporophytes. Geneticists, developmental biologists and evolutionists have been wondering how the switch happened and have put forth two competing hypotheses."

For each hypothesis, scientists have come up with an evolutionary scheme showing how different plant lineages should be related to explain the generation shift. Studies over the last century have produced conflicting results on relationships among early land plant lineages, leaving unanswered the most critical question of how the shift in alternation of generations occurred. Qiu's group used three complementary sets of genetic data, involving more than 700 gene sequences, to resolve relationships among the four major lineages of land plants: liverworts, mosses, hornworts and vascular plants (which include ferns, pines and flowering plants). Their analysis showed that liverworts---tiny green, ribbon-like plants often found along river banks---represent the first lineage that diverged from other land plants when charophyte algae first came onto land, and an obscure group called hornworts, often found in abandoned corn fields, represents the progenitors of the vascular plants.

"Basically we captured a few major events that happened in the first few tens of millions of years of land plant evolution," Qiu said. The results make sense in light of the plants' life cycle patterns. Charophyte algae, liverworts and mosses spend most of the cycle in a free-living gametophyte phase; the sporophyte is a small, short-lived organism that lives on the gametophyte. Vascular plants, on the other hand, spend most of their time as free-living sporophytes, with small, short-lived, gametophytes that often live on the sporophytes. Hornworts may hold a clue to understanding how this shift happened, as they spend most of their life cycle in the gametophyte phase, but their sporophytes---unlike those of liverworts and mosses---show a tendency to become free-living.

Understanding evolutionary relationships among plant groups is crucial to understanding their biology, just as understanding relationships among primates advances our knowledge of human behavior, anatomy and physiology, Qiu said.

"As humans, we're always interested in knowing where we came from and why we are different from other primates," Qiu said. "Now that we know, from phylogenetic analyses, that our closest relative is the chimpanzee, we can compare the chimpanzee genome with our own genome and compare the chimpanzee brain with our own brain and compare chimpanzee behavior with human behavior.

"But this all assumes we know the chimpanzee is our brother. What if we didn't know? Understanding evolutionary history really is the foundation of biology, and with today's emphasis on biofuels and medically important plants, it should be clear how important it is to learn the evolutionary history of all the organisms on our planet."

Qiu collaborated on the project with 20 other researchers from the University of Michigan; the University of Massachusetts, Amherst; the Chinese Academy of Sciences; Universitat Bonn in Germany; the University of Chicago; Southern Illinois University; the University of Akron in Ohio; Freie Universitat Berlin in Germany; Dresden University of Technology in Germany and Harvard University.

Source: University of Michigan

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