Breaking Barriers in Evolutionary Biology: A Pioneering Woman in Science and Her Early Theory of Plant Chemical Macroevolution

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

> It has been suggested to me from botanical sources that time will be unwisely expended over a detailed study of the chemical compounds of plants . . . although it seems to me that many of the vexed questions of plant development [i.e., evolution] can only be solved by a full comprehension of vegetable chemistry. (Abbott 1887, p. 807)

Plant secondary chemistry is now a paradigmatic example of adaptation. However, more than 120 years ago (70 years before the oft-cited works of Fraenkel or Ehrlich and Raven ignited the field of chemical ecology), a female scientist named Helen Cecilia de Silver Abbott (1857–1904) published an article in *The American Naturalist* introducing the radical idea that plant chemistry should be considered in light of macroevolution. Here we revisit the groundbreaking but largely overlooked contribution of Abbott's (1887) "Comparative Chemistry of Higher and Lower Plants." Our goal is to spotlight Abbott's important contribution to the field of chemical ecology and to honor her life as a pioneering woman in science.

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A Simple, Yet Powerful Insight: Patterns of Plant Chemistry Are the Product of Evolution

> The chief idea of the remarks I am about to make is one that has not occupied to any great extent the minds of botanists and chemists, and if it be not true, at least, no other hypothesis has been suggested than the one I will indicate to account for the chemical compounds of the vegetable kingdom. (Abbott 1887, p. 719)

As a young woman, Abbott was eagerly pursuing a career in medicine at the Women's Medical College of Pennsylvania. At age 24, however, a child under her care abruptly died after eating the roots of an unknown wild umbel (Abbott later speculated it was *Conium*), prompting her to first contemplate the diversity of chemical compounds found in plants. This cursory investigation quickly grew into a passion so engrossing it ultimately derailed her medical studies completely. Eager to know more, Abbott systematically accumulated data on chemical compounds found across the plant kingdom. She was sharp and observant, and just four short years later, Abbott transformed the field of plant biology by publishing the first model of plant chemical evolution in her 1887 *American Naturalist* article.

In "Comparative Chemistry of Higher and Lower Plants," Abbott shapes her hypothesis by systematically evaluating metabolite composition in light of plant relatedness, the earliest use of the comparative method to study plant chemistry. In the article, Abbott carefully maps the distribution of major chemicals (e.g., alkaloids, tannins, glucosides, saponins, coumarins) onto the best diagram of plant evolutionary relationships available at the time (fig. 1). Using this approach, she synthesizes several key observations concerning broad patterns of plant chemical diversity. First, she highlights the remarkable amount of chemical variation present

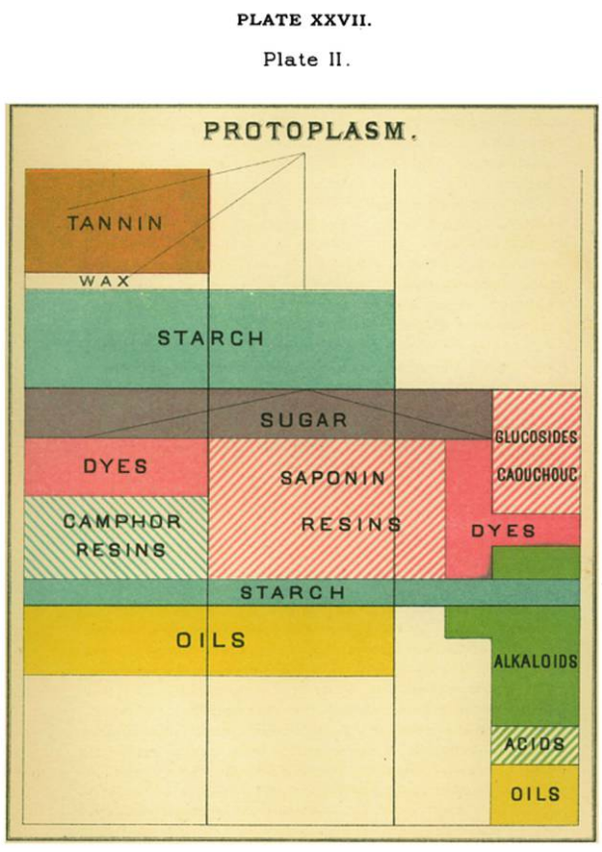

Figure 1: Abbott's figure for the evolution of plant chemicals, based on Eduardo Heckel's morphological evolutionary hypothesis. The three columns represent hypothesized phylogenetic lineages vertically organized by their proposed evolutionary trajectory from simple floral elements, through increasing complexity, and back to simplicity. At each vertical step, the composition of major chemicals can be read horizontally and the evolution of new chemicals traced within a group can be read vertically downward.

in the plant kingdom by summarizing chemical diversity across major plant lineages. Second, she identifies the large-scale tendency for certain chemical compounds in plants to associate with one another repeatedly in different groups. And, finally, she calls attention to seemingly closely related plant species tending to possess very similar chemical characteristics. "It is a significant fact," she states, "that certain cell-tissues or organs secrete or excrete chemical compounds peculiar to them, and which are only to be found in one family or in species closely allied to it" (p. 806). Using these overarching observations, Abbott shapes her prescient thesis: that contemporary plant chemical diversity—both in and among plants—is the product of evolution. Further, she goes on to suggest that future comparative analyses of plant chemistry in light of species morphology and relatedness will prove particularly fruitful for advancing our understanding of evolution.

Indeed, Abbott's "unwise expenditure of time" on plant chemistry and evolution previewed a concept that ultimately spawned a massive field, which has now produced thousands of important articles. Now, comparative studies of plant chemistry are prolific, direct descendants of the tradition she initiated of evaluating plant chemistry in light of a phylogenetic hypothesis. As a result, our current understanding of major concepts in evolution, such as coevolution, adaptive radiation, and mimicry, has been enriched by the tradition that Abbott began.

While the idea that evolution has shaped patterns of chemical diversity across plants is now a well-established fact, we should not forget that, at the time, Abbott's 1887 *American Naturalist* contribution was both brave and novel. Chemistry and evolutionary theory were still in their infancy in the 1880s. Abbott was working with wildly incomplete chemical information and a strangely organized taxonomic hierarchy of plants. A valid mechanism for evolution had not yet been adopted. Furthermore, researchers in the field (including Abbott) maintained a lingering propensity toward *scala naturae* thinking. Despite this, Abbott boldly presented her hypothesis, even while knowing she was out on a limb: "it is not my wish to claim for plant chemistry more than the facts at my disposal will allow," she states, "though in the past, and this should not be overlooked, without the aid of the imagination to penetrate the avenues of the unknown, many of our well-established scientific facts would still be buried from sight" (p. 721). Indeed, Abbott's main tenet ultimately proved true, but it was nearly 70 years until many of the ideas she presented were investigated in depth and some were independently proposed anew (A. T. Tarbell and D. S. Tarbell, 1982, "Helen Abbott Michael: Pioneer in Plant Chemistry," *Journal of Chemical Education* 59:548–549). Now, looking back, it is clear that Abbott's article was truly groundbreaking.

A Bit More Personal History

Beyond her contribution to *The American Naturalist*, Abbott deserves general attention as a remarkable woman in science. Born in Philadelphia in 1857, Abbott initially pursued a career in music, traveling to Europe and performing concerts as a pianist. During this time, she also authored several publications as travel writer, art critic, and poet, beginning what would grow into her long and diverse writing career. She maintained a growing interest in the sciences, however, and in her early 20s, she left the arts to pursue medical school; soon after, she began the study of plant chemistry.

Her seminal 1887 article was published only 4 years after she began studying plant chemistry, making the insight and foresight that she demonstrated even more astonishing. Her decision to publish this work in *The American*

Naturalist was likely due, in part, to the fact that the then editor and part owner of the journal, Edward Drinker Cope, was serving as her unofficial mentor at that time. Based on writings by Abbott soon after Cope's death, it is clear that she had mixed feelings regarding his relationship toward women. On the one hand, she credits his encouragement as influential in her decision to leave medicine and concentrate on plant chemistry (N. H. Dole, 1907, "Biographical Sketch," pages 1–110 in H. C. de S. Abbott, *Studies in Plant and Organic Chemistry*, Riverside, Cambridge, MA). On the other hand, however, she describes his underlying motivations for mentoring women as misguided, stating that he felt that "because she was man's physical and intellectual inferior, [a woman] needed more higher education and . . . [for this reason, Cope] was a woman's warm aider in her scientific work." She goes on to further bemoan Cope's all too common belittling attitudes toward women, stating, "he granted [women's] reason for existence as . . . for man's comfort and perpetuation of the race."

Despite pervasive discrimination against women during that time, Abbott was able to make an impressive and significant contribution to science. She published and lectured broadly. Her ideas of plant chemical evolution were well received and widely esteemed among botanists and chemists in Europe (one article remarked that her work was "the model of a good scientific paper" [Dole]). Her scientific career was ultimately cut short, however, with her investigations into plant chemistry lasting only a decade. After this point, Abbott returned to medical school and, on finishing, briefly opened a free hospital for the destitute of Boston before soon dying of influenza at the age of only 46 (Dole). However, before she died, Abbott deservedly won high acclaim in her day for her work: she was honored as an early fellow of the American Philosophical Society, the American Association for the Advancement of Science, and the Academy of Natural Sciences.

Final Thoughts

> I have attempted to show that the hypothesis of evolution may also apply to the chemistry of plant compounds, and that plant chemistry . . . however [is] exceptional in its broad range, and the variety of its topics, like the variations of flower-species, may be cultivated to suit the taste of the investigator. (Abbott 1887, p. 810)

Abbott's article marks the first explicit use of the comparative method to study plant chemistry and the earliest explicit statement that plant chemical diversity is the result of evolutionary processes. Since its publication, comparative plant chemistry has blossomed into a massive and highly productive field. However, Abbott's contribution has now been largely forgotten. In fact, in the past 50 years, there are only three works citing this article. We hope that this piece will return well-deserved attention to Helen C. de S. Abbott's seminal contribution.

Acknowledgments

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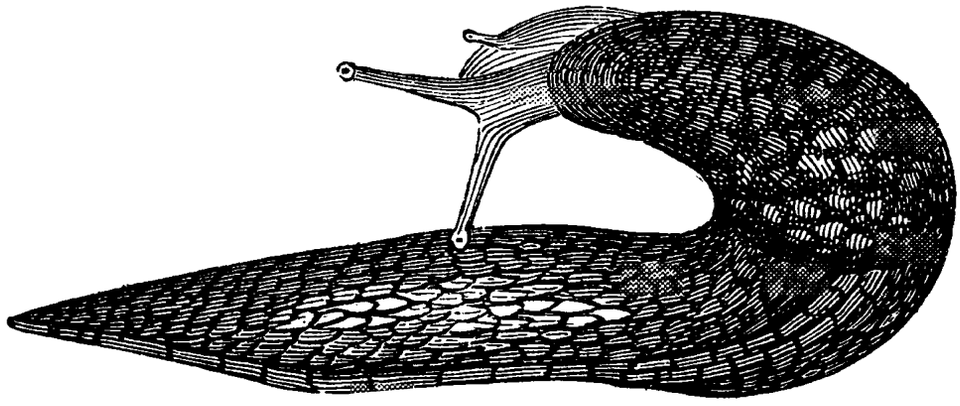
In *The American Naturalist*

Abbott, H. C. de S. 1887. Comparative chemistry of higher and lower plants. American Naturalist 21:719–730, 800–810



"*Limax flavus* . . . grows about three inches long. . . . It is characterized by a brownish color, with oblong-oval uncolored spots; body cylindrical, elongated, terminating in a short prominent keel; mantle oval, rounded at both ends, with rounded spots; base of foot sallow white." From "The Mollusks of Our Cellars" by W. G. Binney (*The American Naturalist* 1870, 4:166–171).