Observation, Natural History, and an Early Post-Darwinian View of Plant-Animal Interactions

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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.*

In 1887, an American botanist, James, published an article on his fascination with milkweeds in *The American Naturalist* (James 1887), becoming one of the first in a long line of plant ecologists who seem to be in love with latex—walking around, breaking leaves, rubbing the sticky, sometimes smelly viscous plant exudate between their fingers. And why not love latex? It is often hard to visualize a plant's defensive tactic, but here is a trait that occurs in nearly 10% of plant species, has independently evolved many times (there are even the latex-bearing mushrooms, *Lactarius* spp.), and seems to have little function other than defense. Latex can therefore serve as a model for understanding the evolution and ecology of many defense-offense interactions. In 1887, James used his observations on the milkweed's latex, herbivory, and pollination, combined with the latest in Darwinian thought, to frame his thinking about plant-animal interactions. Reading this article now offers us remarkable insight into the power of observation and natural history in developing conceptual ideas about an organism's whole ecology, an ideal advanced early on by *The American Naturalist.*

Species Interactions, Latex, and Herbivory

First, James postulated with some certainty that antagonistic species interactions were important in nature: "In spite of the platitudes about the peacefulness of nature, as contrasted with the warfare of mankind, no one can wander through woods and fields without coming, in a short time, to the conclusion that the warfare there is even more severe than it is with the human race" (James 1887, pp. 605–606). To James, competition was of greater importance in animals, while herbivory was more important in plants: "While adaptations of one kind arise among animals to enable them to compete with each other in this struggle, adaptations of another kind are developed in the plant world" (p. 607). Although we now recognize the importance of both competition and enemies for most organisms, James was at the forefront of original thinking about plant defense. Along with studies by Léo Errera and Ernst Stahl published in the late 1880s, James's work led to the origin of plant defense theory.

With specific regard to latex, he wrote: "Serving as a vehicle for the conveyance of nourishment from the roots to the leaves, it carries with it at the same time such disagreeable properties that it becomes a better protection to the plant from enemies than all the thorns, prickles, or hairs that could be provided" (p. 608). James got half of the story correct, the protection part, but like other early botanists, he thought that latex was more or less the blood of plants. When the epidermis is punctured, latex flows out. Upon exposure to air, it coagulates. And with the exception of those specialized to feed on it (think vampires), it does not taste particularly good. But in truth, latex has little other similarity to blood. There is no evidence that it transports nutrients or is otherwise involved in a plant's primary metabolism (A. A. Agrawal and K. Konno, 2009, "Latex: A Model for Understanding Mechanisms, Ecology, and Evolution of Plant Defense against Herbivory," *Annual Review of Ecology, Evolution and Systematics* 40:311–331).

James was clearly very strongly influenced by Darwin's *On the Origin of Species*, published less than 30 years earlier. James (1887) noted that latex of common milkweed (*Asclepias syriaca*; fig. 1) was a remarkably effective defense. At the same time, he noted that "it is a little remarkable that in another species (the Pleurisy Root [*Asclepias tuberosa*]) it is entirely wanting" (p. 612). James observed that despite being free of latex, *A. tuberosa* was highly acrid, and he hypothesized that this acridity was potentially

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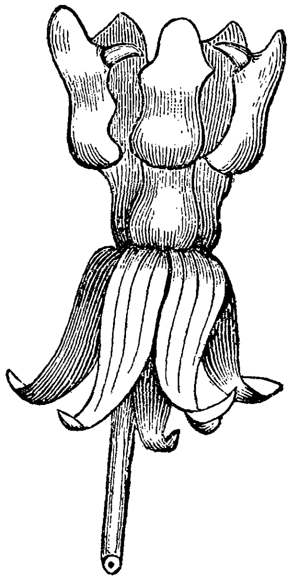

Figure 1: Flower of *Asclepias* enlarged (original fig. 1 from James 1887).

caused by the poor soils where it was found. Accordingly, he was touching on the impacts of resource availability on the evolution of defense strategies, a theme that persists in current studies. Critically, the natural history of species traits, the habitats in which species live, and the interactions they engage in were all critical to his thinking and to the way he developed his hypotheses. Interestingly, James noted that latex and bitter taste (what he called "acridity") were independently expressed: "the amount of milky juice varies in the different [milkweed] species. The acridity of those species which have no milky juice is a sufficient protection, however, from the attacks of herbivorous animals" (p. 613).

James generalized his thoughts on latex by noting that it "is shared in common by a great number of species of widely different orders" (p. 607). In particular, the statement about latex appearing in many taxonomic orders foreshadows what we know about its convergence. Latex arose independently tens of times, about the same number of times as C_4 photosynthesis. And yet, for such a highly convergent trait to show tremendous intrageneric variation posed a mystery to James. Indeed, we still do not have strong hypotheses about the drivers of variation in latex seen among closely related species.

More generally, much of modern comparative biology is focused on assessing the relative importance of shared evolutionary history (phylogenetic signal) and convergence or divergence, which we would like to implicate in adaptation. One possible explanation for the variation in latex production is that plant species coevolving with herbivores are likely to escalate their levels of defense, such as latex, while other species are not. Although trait matching in plant-herbivore species pairs is common (i.e., defended plants having herbivores capable of tolerating those same defenses), stronger evidence for coevolution is usually wanting.

Exactly 100 years after James's article was published, D. E. Dussourd and T. Eisner showed the highly convergent behavior of specialist insects that sever latex-delivering canals (laticifers) of milkweed before chewing the leaves (1987, "Vein-Cutting Behavior: Insect Counterploy to the Latex Defense of Plants," *Science* 237:898–900). Their natural history observations alone are the stuff legends are made of, and with the addition of simple experiments, the inferences they made were profound. Producing latex must be costly to the plant, and behaviorally deactivating laticifers is certainly costly for herbivores. Thus, even though any one milkweed insect wasn't the evolutionary driver of latex evolution, at least in a diffuse sense, these herbivores and plants appear to be coevolving. A continued combination of comparative and experimental approaches on both plants and herbivores could be highly informative for understanding the sequence of evolution, function, and potential drivers of traits involved in coevolution (M. G. Weber and A. A. Agrawal, 2012, "Phylogeny, Ecology, and the Coupling of Comparative and Experimental Approaches," *Trends in Ecology and Evolution* 27:394–403).

Reproductive Biology

In addition to the milkweeds' insect herbivores, James devoted his observational skills to milkweeds' flower visitors, with a keen eye toward understanding the plant's reproductive biology. He described the pollination system, akin to only that of the orchids, in which pollen grains are packaged in sacs called pollinia. He observed that when insects, attracted to the smells and nectar of flowers, scrambled over milkweed flowers, pollinia became attached to their legs (and later were inserted into flower slits to consummate pollination). Some of these floral odors are sweet, while others are putrid, the latter of which attract carrion flies, duping them into pollination services.

In addition to noting the identity of flower visitors, James (1887) observed that "[n]otwithstanding the numbers of insects frequenting the flowers, it is noticeable that only a few of them produce seed" (p. 611). Indeed, since James's time, milkweeds have been well studied for their remarkably high flower-to-fruit ratio (R. Wyatt and S. B. Broyles, 1994, "Ecology and Evolution of Reproduction in Milkweeds," *Annual Review of Ecology and Systematics* 25: 423–441). That is, despite having hundreds and hundreds of flowers, most plants set very few fruits. That this pattern was not lost on James is a testament to his observational skills.

Final Thoughts

Joseph F. James was not an experimental biologist. And yet his sharp sense of observation, natural history, and comparative ecology led him toward conceptual ideas and hypotheses. There is tremendous potential in his way, especially when coupled with more modern approaches (Weber and Agrawal 2012). For example, experimentally manipulating latex in multiple species (that vary in trait expression) while transplanting them across habitat types could inform us of the relative function of such a trait, among the ecological contexts where species naturally exist. Naturalists' knowledge should not only be enjoyed but encouraged among our students and, whenever possible, integrated into our theories and hypothesis testing. Whether we add on modern approaches, the classic methods of observation, natural history, and comparing species will always be an important part of the big questions in biology.

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Asclepias latex. Photo credit: Ellen Woods.