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Endless Symbioses Most Intricate*

Article and photographs by W. John Hayden, Botany Chair

When I was much younger than I am now, I enjoyed reading science fiction. Much of what I read so long ago is irretrievably lost in the nooks and crannies of memory. But one story left in me a lasting impression. I can remember neither title nor author, but the plot involved, as usual, intrepid explorers discovering alien new worlds. One such exploration involved a world bathed in an ocean teeming with life. Initially the biologists among the spaceship crew were eager to retrieve samples, but everything they tried to pull out of the ocean was attached to something else. Big kelp-like algae were intimately entwined with lobster-like animals that were, in turn, connected to other life forms, and those to still others, and so on. All efforts to retrieve a single specimen failed, because every organism in that fictional watery world was physically connected to every other. As described in the story, this world of total symbiotic connection intimidated and repulsed the explorers, who soon blasted off to other worlds and other adventures.

Like the characters in the story, I found the story's depiction of rampant symbiosis and interconnectedness of species to be disturbing, at least initially. Perhaps what troubled me stemmed from the fact that, at that time of life, as young people do, I was busy constructing my own sense of self, whereas the creatures on that alien planet seemed to have scarcely any vestige of self or individuality. At that same time, I was beginning to learn about the life forms of planet Earth by poring through field guides—both the Golden Guides and Peterson series were important to me in those days—and the glimpses of life on this, my own planet, as depicted in these field guides, clearly emphasized the individuality of species. That fiction-al watery world of pervasive symbiosis was just shockingly strange to me at that time.

But I am older now, and I have learned a lot more about life on planet Earth since reading that science fiction story. And that fictional world no longer seems as strange to me as it once did. Most life forms on Earth are not as connected in a direct and physical way as those depicted in the story, but the creatures of Earth are most certainly connected ecologically; all are part of the web of life. Each species impacts many others.

Orchids, such as our Wildflower of the Year for 2016, Downy Rattlesnake Plantain (*Goodyera pubescens*) (Fig. 1), exemplify the interconnectedness of life on Earth. As would be the case for many kinds of plants, pollination comes readily to mind as a prominent example of mutualistic symbiosis. Downy Rattlesnake Plantain is pollinated by bumblebees and other native bees. The bees gain nectar and the orchid gets an efficient means to move pollen from one flower to another; each organism gains benefit from the interaction, the very definition of mutualism. Pollination by bees is widespread among the orchids, but there can be much variation in the nature of the pollinator reward (nectar, resin for building nests, and fragrance for attracting mates), and the choreography of bee behavior in the flower is as varied as the sizes and shapes of orchid flowers.

If pollination is successful, and it often is for Downy Rattlesnake Plantain, the result is a capsule full of seeds. Orchid seeds are minute, dust-like, and easily dispersed by wind; they are also produced in prodigious numbers. Small, light-weight seeds, however, cannot contain much in the way of stored food for the future seedling. In fact, orchid seeds have essentially no stored food at all; they consist merely of a thin seed coat and a tiny embryo (Fig. 2). It really does take a microscope to perceive them in detail.

So how do orchid seedlings get established without a stash of food to draw upon for their earliest efforts at existence? To answer that question it must first be acknowledged that many orchid seeds simply perish. Passive dispersal by wind will drop many seeds in spots not at all favorable for growth. A lucky few, however, will come to rest in a spot with

Figure 1. Downy Rattlesnake Plantain, Goodyera pubescens.



Figure 2. Seeds of Downy Rattlesnake Plantain as viewed through a compound microscope. The dark central mass of cells is the embryo; thin-walled empty cells constitute the seed coat.



Figure 3. Some tropical epiphytic orchids. From Asa Gray's How Plants Grow: A Simple Introduction to Structural Botany (New York: American Book Company, 1858).

adequate moisture, some—but not too much—light, and one more essential ingredient: the right fungus.

Initial stages of orchid seed growth may occur without fungal interaction, but to continue growing and developing the orchid embryo must encounter a fungus that penetrates the seed and interacts with the embryo. Not all contacts between an orchid and its symbiotic fungus work. Sometimes the fungus consumes the orchid just as any pathogenic fungus digests cells of its host plant. Sometimes the orchid kills the fungus, and, if so, the baby orchid soon dies of starvation. Other times the orchid and fungus are compatible, and orchid cells are able to obtain essential nutrients from the fungus, permitting it to grow, albeit slowly at first. When a successful symbiosis is established, the fungus and orchid embryo form a structure called a protocorm, a slowly growing ball of orchid cells and fungal hyphae (chains of fungal cells). It can take weeks to more than a year for the little green protocorm to acquire sufficient nutrients from its fungal associate and grow large enough to form its first root and leaf-and once a leaf has formed, the baby orchid can begin the process of photosynthesis in earnest. The situation is analogous to mycorrhizae, but the orchid seed tissue penetrated by the fungus is not a root and it is difficult to imagine that the minute orchid embryo has much to give the fungus. But once the seedling makes leaves and roots, mycorrhizae in the strict sense can form, the orchid receiving mineral nutrients from the fungus and the fungus receiving carbon compounds formed by photosynthesis in the plant. It is sobering to think that every orchid you encounter in nature owes its very existence to early nutritional assistance from a fungus.

Many orchids, especially those in the tropics, cling to life on the bark of a tree (Fig 3). Such species are termed epiphytes, and the symbiotic relationship between orchid and tree is characterized as commensal, beneficial for the orchid, but with neither benefit nor detriment to the tree. Epiphytic orchids are not parasites; their roots penetrate only the most superficial layers of bark, and the orchid receives no nutritional benefit from the tree. In extreme cases, however, heavy epiphyte load on a tree can lead to the breaking of branches or the interception of significant amounts of sunlight that would otherwise have illuminated leaves of the tree. In most cases, however, presence of a few epiphytes is of no consequence to the tree.

Other orchids, like Downy Rattlesnake Plantain, are terrestrial, rooted in soil. As any organic gardener will tell you, soils are (or should be!) swarming with microbes (bacteria, protozoa, algae, invertebrates, and so on) and macroscopic life forms (worms, insects, burrowing vertebrates). It is life in the soil that controls the cycling of mineral nutrients and the penetration of oxygen and water between soil particles. Terrestrial orchids, like all higher plants, benefit greatly from activities of myriad life forms in soil.

Of course, not all interactions between plants and other species help the plant. Many woodland orchids, including Downy Rattlesnake Plantain, and especially their flower stalks, are relished by deer. In this case, the orchid's lost reproductive potential is the browsing animal's gain, i.e., a nutritious morsel of food. And it is not just the occasional deer that eats or preys upon or infects orchid plants. All sorts of hungry insects and pathogenic fungi and bacteria are ready, willing, and able to convert orchid biomass to that of their own species. Sometimes the orchid wins, sometimes it loses, but win or lose, the life of an orchid is inextricably intertwined with a multitude of other species.

This essay has focused on connections between orchids and other forms of life. Similar stories of ecological connectedness could be told for any species, only the details would differ. Life on Earth is, indeed, woven into a complex fabric. What might first appear to be an individual organism will prove, on careful study, to be one of the numerous interconnected threads that make up the tapestry of life. And that tapestry, followed with patience and persistence, will be found to encompass the entire biosphere—much like the alien life forms in that story I read so long ago. Little did I know then that a piece of juvenile fiction would become central to my understanding of biology. *****

*The title echoes "... endless forms most beautiful ...," words used by Charles Darwin in the closing passage of his Origin of Species.

WHAT DID JOHN MUIR SAY?

A wonderful quotation sums up the pervasiveness of symbioses among the life forms of Earth: "When one tugs at a single thing in nature, he finds it attached to the rest of the world." This aphorism is commonly attributed to John Muir, and it certainly sounds like something he might have said. Unfortunately, according to the Sierra Club-and they ought to know-these are not the words of their founder. What Muir wrote is, "When we try to pick out anything by itself, we find it hitched to everything else in the universe." The same sense is there, but the compass of Muir's actual words is far greater and, consequently, their pertinence to the ecology of the blue marble that we call home is less direct, less compellingwhich, no doubt, explains the popularity of the misquoted version. For a discussion of Muir's words on this subject, actual and misquoted, see: http://vault.sierraclub. org/john_muir_exhibit/writings/misquotes.aspx �