An Ethnobotany of Darwin's Gardens

Nina L. Etkin

Research

Abstract

This article puts a unique spin on Charles Darwin's work by looking at the plants that he studied through the lens of ethnobotany. I employ this biocultural perspective to explore a handful of species to understand how their cultural constructions intersect their physical appearance, biochemistry, and behavior. While Darwin's natural history studies contemplated variation, sexual reproduction, speciation, and a myriad of other biological themes, I look at the conjunction of ethnography and the biology of therapeutic and other actions to describe how diverse cultures use those species for medicine, food, and other applications, and how their tangible qualities both impact health and contribute to meaning. I briefly introduce Darwin and his theory of natural selection and his impact on science and society. Following, I problematize two groups of his plants to which I apply the same theoretical perspective – what many (but not Darwin) regard to be "prosaic" garden species, and the striking insect-trapping plants.

Introduction

Current discussions of Charles Darwin are timely and emerge from all sectors: the year 2008 marks the 150th anniversary of the presentation of Darwin's and Alfred Russel Wallace's work to the Linnean Society of London; in a few months' time, 2009 will overlap the 150th anniversary of the publication of Darwin's *Origin of Species*, and his 200th birthday. This article draws from my book-length manuscript, currently under publishers' review, which explores many of Darwin's species through a broadly ethnobiological perspective. The manuscript is comprised by discrete chapters on Darwin's theoretical advances in the context of Victorian science and society, domesticated garden species, orchids, insect-trapping plants, plant movements, and animals. It draws on diverse literatures that span botany, anthropology, history, phytochemistry, and pharmacology.

Charles Darwin's theory of evolution is based on the premise that all life is connected through shared ancestry. "Unlike most great scientists of the past, whose work has been absorbed by science (and often by culture) and marked as a brilliant stage toward later developments, Darwin remains strangely and almost charismatically alive" (Levine 2000: ix), and evolutionary biology is still a beacon of the intellectual struggles that enliven and transcend the sciences. In *Darwin's Plots*, Beer describes *Origin of Species* as "one of the most extraordinary examples of a work [that] included more than the maker of it at the time knew, despite all that he *did* know" (Beer 2000: 2). A valuable resource and the most comprehensive treatment of Darwin is *The Complete Works of Charles Darwin Online* (2008), a scholarly website that covers more than 40,000 pages of searchable text that are available in PDF format.

On the Origins of Darwin

While Darwin was an avid collector from a young age, his most transformative experiences occurred during his five-

Correspondence

Nina L. Etikin, Department of Anthropology
University of Hawai`i, 2424 Maile Way
Honolulu, Hawai`i, 96822. U.S.A.
etkin@hawaii.edu

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year service (1831-1836) as naturalist for Captain Robert FitzRoy aboard the H.M.S. *Beagle*, which was commissioned by the British admiralty to circumnavigate the globe to secure British commercial, imperial, and military interests in the New World; establish standard cartographic measurements; and survey the harbors and coasts of South America and the Galapagos Islands. The voyage extended to South Africa and the South Pacific as well. Much of Darwin's time was spent on land, where he recorded geologic features and collected a huge number of specimens, many of which formerly had not been described by Europeans. Through these ventures, he came to appreciate the geo- and biodiversity of much of South America. He supplemented his collections with descriptions that he elicited from local residents and specimens collected by the *Beagle*'s crew. This conscientious approach became the signature of this masterful naturalist.

Rather than isolating Darwin from the elite scientific community, the long *Beagle* voyage helped him to establish a position in its inner circle: by the end of the journey, Darwin – still in his twenties – had distinguished himself among naturalists of authority through correspondence and the many collections he sent to Cambridge. As England and Europe approached mid-century, most who could afford to, or were sponsored, collected plants and animals on scales of great size and diversity. But Darwin and only a few others engaged the intellectually charged work that made theoretical advances.

All Naturalists Great and Small

The Darwinian "revolution" was not solely a product of Darwin: no one more than he understood the contributions of many and the incremental growth of knowledge. The individuals who had the most intellectual impact on Darwin include Carolus Linnaeus (1707-1778) who developed a classificatory system for all life forms, the foundation for which is binomial nomenclature. In *Essay on the Principles of Population* (1798), Thomas Malthus argued that while human population growth is exponential, food supplies increase only slowly; as competition is inevitable, only some individuals survive. Jean Lamarck (1744-1829) drew attention to adaptations to environmental circumstances. Charles Lyell (1797-1875) emphasized the temporal depth that informed Darwin's vision of gradual change over extended time.

Darwin's notes from the summer of 1842 include his early outline of a theory of evolution and his first use of the term "natural selection." Two years later, he recorded a more fully formulated theory, which itself continued to evolve throughout his lifetime. During all the years after return of the *Beagle*, Darwin designed experiments, moved information around in increasingly sophisticated theoretical models, and wrote prodigiously. By the mid-1850s, several of Darwin's closest colleagues were both impressed and persuaded by his theory; but some scientists, and certainly the public, found it difficult to reconcile humans as part of a comprehensive evolutionary process. His theory soundly unseated the image of the "dignity of man," a centuries-old credo that was part of the Victorian ethos.

Charles R. Darwin and Alfred Russel Wallace

The name most commonly paired with Charles Darwin is Alfred Russel Wallace (1823-1913), whose work, arguably, is the most significant factor that moved Darwin toward publication. In June 1858, Darwin received from him a manuscript that detailed a theory of evolution by natural selection that was virtually identical to Darwin's own. One month later, their work was presented to the Linnean Society of London as a combination of Darwin's long-standing ideas on evolution and Wallace's sketch on the same topic. It was later published in the *Journal of the Linnean Society*.

By September of that year, Darwin began seriously to edit down his long work into a more succinctly argued format and finally completed *Origin of Species* in May 1859. It was published six months later and met considerable resistance worldwide. The reverberations extended well beyond the scientific community: politicians, the clergy, and the literary and fine arts responded. Great interest in the book was evident as people read it on public transport and borrowed copies from England's largest circulating library. The stock sold out the first day, the publisher hastened a new run of 3000 copies, after which it was reprinted many more times.

Why such a sensation? More than Wallace, more than anyone else, Darwin's *Origin of Species* was powerfully persuasive because it embodies encyclopedic evidence. His observations, reading, and experiments range among all manner of evolutionary relationships: everywhere, he sought and confirmed patterns. Where others described and a few offered mid-level theories, from Darwin's analysis emerged higher order abstractions and sophisticated theory grounded in universal and unifying principles. By less than a decade after publication of *Origin of Species*, the fury had subsided.

As this background discussion establishes, Darwin was a discriminating observer at several scales, from the great variety of organisms studied to details of morphology, physiology, and behavior. From the thousands of plants that Darwin studied, I describe several "garden variety" (prosaic) species that I juxtapose as a category to dramatic insect-trapping plants. In this ethnobotanical exploration, I offer general characteristics to highlight themes that frame Darwin's studies, and cast cultural constructions of those plants against the backdrop of morphology and phytochemistry.

"Prosaic" Garden Plants

By the 1700s, naturalists had distinguished female and male structures in flowers but did not understand their morphology or the biology of their reproduction. In *Sponsalia Plantarum* (1746: 103), Linnaeus's scandalous reference to the calyx as a "bride chamber" perpetuated the misapprehension that most plants are monoecious and self-fertilize (the Latin *sponsalium* approximates "marriage"). Although botanists of the next century compiled increasing evidence for insect pollination, a better apprehension of flower structure and function did not coalesce until Darwin began publishing his observations in the 1860s. Almost three decades earlier, he had already deduced that self-fertilization – which fosters homogeneity – belies the evidence of variation, selection, and evolution.

In spring 1860, Darwin identified dimorphic flowers in the English primrose, *Primula vulgaris* Huds. and the cowslip, *P. veris* L. (Primulaceae). His experiments confirmed a reproductive strategy in which selection favors cross-pollination between short-style and short-stamen flowers, and between their long counterparts. He first hypothesized, erroneously, that these species were inclined toward a dioecious habit in which unisexual reproductive structures occur in gynoecious and androecious plants. But further experimentation with seedlings transplanted to garden patches and covered with netting illustrated that the species were monoecious.

While botanists of the day regarded insects and wind to have the same valency for pollination, Darwin noted the obvious flaw in this reasoning. In both dioecious and monoecious species adapted to insect pollination, an "endless number of adaptations" are permutations on color, scent, location of male and female structures, anatomical modifications, response to physical stimulation, and tropisms. Darwin noted that wind-pollinated rhubarb (*Rheum* spp., Polygonaceae) and spinach (*Spinacia oleracea* L., Chenopodiaceae) produce great clouds of pollen dust. Conversely, insect-pollinated species are more efficient, accommodating a range of bees (Apidae) and other taxa on whom they deposit dense pollinia.

Darwin learned about the specificity of associations between plants and their pollinators, describing, for example, how the cochineal insect (*Dactylopius coccus* Costa, Dactylopiidae) thrives only on the native South and Central American variants of prickly pear cactus (*Opuntia* spp., Cactaceae), and not on those that have been exported to other parts of the world. (Today, cochineal insects thrive on prickly pears worldwide.) In this case, mutualism involves insects drawing moisture and nutrients from the cactus, and using the plant tissue as a substrate for nymph growth. In turn, they secrete carminic acid, which deters predation by other herbivores. Another refinement occurs in blue flax (*Linum perenne* L., Linaceae): as in golden and scarlet flax. (*L. flavum* L. and *L. grandiflorum* Desf.), the stigmata surfaces of blue flax are oriented toward the flower center, but only in the bud stage. When the flower is completely open, the alignment shifts so that the five stigmata face about, and each produces a drop of nectar that draws in the pollinator.

Insect-Trapping Plants

For centuries, biologists have been intrigued by the anatomy and ecology of insect-trapping plants, species of striking appearance whose leaves are specially modified traps that serve animal attraction and nutrient capture. Recognized scholars consider that since the early 1600s, when careful academic study of insect-trapping plants began, there have been published only "two major works in English" (Juniper ***et al***. 1989: ix): Darwin's *Insectivorous Plants* (1875) and Lloyd's *Carnivorous Plants* (1942). Darwin's exacting experiments demonstrated that these plants are well adapted to trapping insects and do so regularly, that digestion occurs, and that nutrient assimilation benefits the plants as gauged by their health, growth, and reproduction. He also described microscopic changes in tissues that accompany the attract-trap-retain-digest-assimilate process.

Whereas mucilages, attractants, and other features occur throughout the plant world, in insect-trapping plants, they are concentrated and synchronized in a limited part of the plant. Technically, the historical definition of these plants excludes those that rely on other arthropods or microorganisms for digestion, or that do not attract insects, but over the last few decades, the definition of trap plants has become more inclusive: other taxa have been added to this functionally generalized group that exhibits an adaptive model that is present across a broad spectrum of Angiosperms. Literature published during the last decade is even more theoretically refined and contextualizes complex interspecific and other ecological relationships.

Insect-trapping plants derive nutrients, notably nitrogen, by attracting, trapping, killing, digesting, and assimilating protists and animals, primarily insects and other arthropods. Some assimilate as much as fifty percent of their nitrogen and phosphorus from insects (Plachno *et al*. 2007). All are self-sufficient for energy, which they generate by photosynthesis, and engage other processes of primary metabolism. Collectively, as for other characteristics, insect-trapping plants represent a spectrum of heavy to low dependence on arthropods, which varies with life form, individual, and ecology .

Generalizations about digestion in insect-trapping plants include evidence for glandular phosphatase, esterase, and protease activities. Extracellular phosphatase and other enzymatic activity also has been detected for trapped and symbiotic insects, bacteria, fungi, and algae. Many insect-trapping plants are associated with specific insects which, although they use some of the nutrient resources, produce frass from which the trap plant can assimilate nutrients. Insect attractants in plants generally, and in traps, include combinations of fragrance, pigmentation, and nectar

Categorization by trap mechanics organizes the discussion below and offers a structural/functional classification that ranges from simple to elaborated chambers and their appurtenances and embellishments. Traps, secretory and digestive glands, and other components are a complex suite, rather than discrete and single characters. My template describes categories of trap plant, but species, or even individuals, might deviate from those generalized models. Two cases in point are that trap architecture of the same species might vary with epiphytic, terrestrial, and aquatic life forms; and many trap structures, such as bristle appendages and thresholds are rudimentary or absent in some species (Reifenrath *et al*. 2006)

Except where otherwise indicated, the following discussion of plant anatomy, metabolism, nutrient capture, and ecology draws from Darwin (1875), Lloyd (1942), Juniper *et al*. (1989), Schnell (2002), the Australian Carnivorous Plant Society (2008), the Botanical Society of America (2008), and the International Carnivorous Plant Society (2008).

Pitfalls

Darwin's interest in insect-trapping plants emerged from his more generalized curiosity about plant movement, to which he devoted considerable investigative energy. He was fascinated by pitcher plants whose traps are some of the most dramatic structures in the plant world. Late nineteenth-century amateur naturalists' claims that pitcher fluids have "intoxicating and anesthetic" effects on insects in all likelihood bear on the production of digestive enzymes. Among trap plants, the Sarraceniaceae and Nepenthaceae are the largest and best characterized families. The fluids of immature traps are sterile. Soon after the pitcher opens, the cuticle that overlies glands of digestion and assimilation dissolves, and the phytotelma fills with intrinsic enzymes and bacteria that are washed in with rain water. Individual pitchers experience a regular succession in protozoan, bacterial, and dipteran resident species (Miller & Kneitel 2005). Unlike other trap plants which capture episodically, pitchers do so continuously. Digestive activity increases in older pitchers, in part the result of increasing titers of microorganisms that contribute to enzymatic degradation.

The genus *Sarracenia* includes small New World pitchers, numbering about ten species. Zone one of the purple pitcher, *S. purpurea* L., is a lid that is compactly lined with down-pointing hairs and punctuated by nectar glands and red venation, which might be an attractant. *Sarracenia* opercula are pocked with areolae. Insects that enter the pitcher exhaust themselves trying to exit via these mock windows and eventually drop into the phytotelma. The second, conducting, zone has slick walls with down-pointing extrusions and attracts insects with glands that deliver very apparent nectar drops. The next, longest, zone has a slick surface and many glands that secrete digestive enzymes. Down-pointing hairs in zone four restrain insects while digestion and assimilation occur.

The family Nepenthaceae is represented by a single genus of traps, *Nepenthes*, monkey cups, which is distributed throughout insular and peninsular Southeast Asia. The genus embodies much variation in pitcher form and associated arthropods. Features common to virtually all *Nepenthes* species are the pitcher, a true leaf which hangs from a tendril that grows as an extension of the leaf midrib; a pair of fringed wings on the pitcher front; a lid; and the peristome, a ridge of hardened tissue around the rim. In addition to bright pigments, many *Nepenthes* species also have strong ultraviolet contrast patterns which draw in insects that rely also or more on that portion of the light spectrum. *N. reinwardtiana* Miq. traps have two clear, round, "eyespots" in the upper pitcher, analogues to the areolae of *Sarracenia*.

The upper, conductive zone of *Nepenthes* pitchers is sheathed by wax plates that do not allow insects to gain purchase, increasing the likelihood that they will fall into the phytotelma in the lower pitcher. Glands that secrete digestive enzymes line the lower pitcher. The fluids of some species contain wetting agents, another adaptation that makes insect escape difficult. Digestion is accomplished by the combined action of enzymes and larvae of insects that are adapted to phytotelma environments, including in *Nepenthes* species, very low pH. Larval feeding increases the surface area on which pitcher enzymes act. Adult midges, flies, mosquitoes, and other insects lay eggs in newly opened pitchers, larvae remain in the pitchers through their juvenile stages, adults that emerge after pupation leave the pitchers.

Adhesive Traps

The principle of flypaper traps is numerous stalked mucilage-secreting glands that constellate the plant's leaves. *Pinguicula* species (Lentibulariaceae), butterworts, are native to the northern and southern hemispheres. The leaves respond to insect contact by rapid growth, movements that involve creating a concavity under the insect, which serves as a digestive site, or rolling the leaf, which prevents rain from washing the insect away. Darwin (1875) timed the curling to an average of two and one-half hours. The tips of stalked glands secrete mucilage that encumbers insects. In some species, the gland also secretes amylase. Nutrient assimilation at the base of sessile glands begins as early as two hours after stimulation, the process is complete and leaf architecture is restored within three days. Given the diminutive size of the glands, arthropods that are associated with this genus are small, primarily gnats and midges.

Darwin's experiments with the northern temperate sundew *Drosera rotundifolia* L. (Droseraceae) were the foundation for establishing insectivory as a means of nutrient capture. More than 170 species of *Drosera* also have active traps: every leaf is covered with 150-200 upright stalked glands each of which is tipped with a drop of mucilaginous fluid that contains digestive enzymes. Plant growth following stimulation by insects assists their restraint and digestion. When an individual becomes trapped by the secretions, the glands bend inward toward the trap center and surround the insect. This is the rapid phase, which Darwin timed as three to twenty minutes. In a slow phase, stalked glands that the insect has not contacted also bend, contributing their secretions to the trap. In some *Drosera*, a second slow phase includes trap folding. Leaf bending, and to some extent the participation of additional stalks, represent hormone-mediated growth: auxin is produced in response to the capture stimulus. Numerous small sessile glands are present as well. Mucilage glands at the trap margin secrete esterase, acid phosphatases, and protease. The hairs release chitinase (Matusikova *et al*. 2005) and other enzymes, and resume their original position when decomposition is complete, within a few days. Resident bacteria also produce digestive enzymes. That dust and other inorganic debris elicit virtually no hair response reflects that the sensitive hairs distinguish nonfood from protein-containing food. A substantial portion of *Insectivorous Plants* (Darwin 1875) is devoted to *Drosera*, whose movements so intrigued Darwin that he wrote "I care more about *Drosera* than the origin of all the species in the world" (Darwin Online 2008). The cosmopolitan sundew is most diverse in Australia and occurs on all continents except Antarctica. It ranges in size from the three-foot-long leaves of the South African king sundew (*D. regia* Stephens) to the three-quarter-inch round rosette of the pygmy sundew of Australia (*D. nitidula* Planch). The sundew bug (*Setocoris* spp., Miridae) is associated with these plants and provides assimilable nutrients in its frass.

Lobster Traps

Darwin described *Genlisea* (Lentibulariaceae) species from West Africa and South America as small, rootless plants that trap aquatic or soil organisms. The trap of the corkscrew plant is characterized by a stalk, a vesicle, and a neck (hollow channel) that splits into two twisted arms that are lined with glands and hairs. The basic principle is a cavity that is easy to enter and is either lined with inward-directed thorn-like filaments or the exit is difficult to find. *Genlisea* attract and trap diverse protozoan and metazoan fauna; many specialize in aquatic species.

Suction Traps

Unique to the ubiquitous bladderwort (*Utricularia* spp., Lentibulariaceae), suction traps are highly modified leaves that hang from stolons by short stalks. Representing some 215 species, the bladder-shaped traps have a hinged opening around which bristles and appendages are positioned. Stalked glands at the aperture secrete mucilage, but this does not trap insects. On stimulation of trigger hairs, ions are moved out of the utricle, water follows, creating a partial vacuum. The opening is set askew when the triggers are disturbed by invertebrates, who are sucked into the utricle, with water, as the vacuum is released. As digestion proceeds, interior glands assimilate nutrients and contribute to water resorption as the trap is reset. Darwin observed that among trap plants, bladderworts have the most morphologically and functionally complex and fast-closing traps. Some intrinsic enzymes are produced. It has been speculated that, in view of the presence of diverse microorganism communities, bladderworts that have low trapping volumes due to limited insect availability might benefit more from commensal enzymes and frass than the digestion and assimilation of insects.

Snaps

The aquatic waterwheel (*Aldrovanda vesiculosa* L., Droseraceae) and terrestrial Venus flytrap (*Dionaea muscipula* J. Ellis, Droseraceae) have hinged leaves that snap closed when sensitive hairs are touched. In both plants, the terminal (true) leaf of a flat petiole is bilobed, with a hinged midsection that snaps the trap when stimulated by insects. As insect movements stimulate the lobes' internal surfaces, the lobes grow toward one another, sealing the insect into a pouch in which enzyme-assisted digestion proceeds for one to two weeks. *Aldrovanda* traps are supported on petioles with air bladders that aid flotation and are lined with fine trigger hairs. Phosphatases are present in all glands, and in high titers in quadrid hairs. Darwin referred to the receipt of a waterwheel study specimen as "a magnificent present" (Darwin Online 2008).

Native to North and South Carolina, the Venus flytrap is structured by rosettes of four to seven leaves that average three inches in length, and after flowering are replaced by longer leaves that carry traps. The lobes of the trap secrete mucilage and are pigmented with anthocyanins. Insects are attracted to the trap margins where nectar is secreted. Three hair-like trichomes on each lobe detect insects, but not in the generalist patterns described for some other trap plants. Venus's specialized mechanism distinguishes live insects from other stimuli such as wind-borne particles or rain: a snap is triggered if one trichome is touched twice or two are touched in succession within 20-40 seconds. The very rapid, one hundred millisecond-closure (Forterre *et al*. 2005) elicited from Darwin the judgement that "this is one of the most wonderful plants in the world" (Darwin Online 2008).

Trigger Plants

Of the 300 *Stylidium* species (Stylidiaceae) nearly endemic to Australia, some unknown percentage attract and trap insects. Male and female flowers are fused into a pillar-shaped tube. When stimulated by an insect, a shift in column turgor results in a snap forward, which showers the insect with pollen. Darwin described this movement of the gynostemium as "circumnutation," which occurs in other plant parts as well, tendrils for example. Glandular trichomes on flowering stems, sepals, leaves, and flowers trap insects, digest proteins, and assimilate amino acids. Constituent proteases have been reported; although no phosphatase activity has been recorded, it is possible that the enzyme is produced only when the plant is stimulated.

The biologies of these two groups, garden varieties and insect-trapping plants, are familiar to many botanists. Here, I return to the unique contribution that this paper makes to the literature by casting those biologies in a biocultural perspective. In the discussion that follows, I further contextualize Darwin's species by adding cultural, pharmacologic, and nutrient data to the mix.

Ethnobotany

The criteria that I established to identify for ethnobotanical inquiry a subset of the aforementioned Darwin's species include reliable scholarship on the ethnography, physiologic actions, and nutrient and pharmacologic potential of those taxa. Compilations that I consulted for general information include Mabberly (1993), Moerman (1998), Therapeutic Research Faculty (2003), Yarnell *et al*. (2003), and PDR (2004). Unless otherwise stated, medicinal applications and other uses reference European, English, and North American customs of the last few centuries, including native groups. I write in the present, since many of these today are used again – or still – in homeopathic, naturopathic, complementary, and integrated medicines.

Garden Varieties

Cowslip flower and root are used medicinally for bronchial impairment, cardiac disorders, pain, and neurological symptoms. The root is applied topically for headache. In both structures, flavonoids (quercetin, kaempferol, others) and saponins (primulic acid) effect diuresis and expectoration. Flavonoids also can be anti-inflammatory and antispasmodic. Primetin and other methoxyflavones in *Primula* species are antiviral. Cowslip can potentiate the effects of sedative and diuretic drugs; proteases purified from the plant are used in the food industry. In some species, primetin induces contact dermatitis; researchers speculate that other sensitizing flavones may occur as well. Other primulas are used to flavor grape wines, and their flowers are the fermentation substrate of cowslip wine. The medicinal uses of primrose are similar to those of cowslip. Like many plentiful, colorful flowers, cowslip and primrose decorate Maypoles and other icons of spring. The leaves and flowers of cowslip and other species are edible, serving as cold salad and soup ingredients (Demir *et al*. 2007, Huck *et al*. 2000).

Flax plants (especially *Linum usitatissimum* L., common flax), including seed and its oil extracts, are exploited for the laxative effects of galactans and other mucilages. In India and among Native North Americans, the seeds also are used for gastrointestinal and respiratory disorders, topically for skin infection and inflammation, and to remove foreign bodies from the eye. Decreases in blood sugar and cholesterol are suggested. Antitumor activity is attributed to antimycotic, antiestrogenic, and antioxidant lignans (enterolactone and enterodiol). Several flax species are used by Native North Americans for gastrointestinal and kidney disorders. The same groups use the seeds of several flax species for cooking, and the roots and stems for cordage and basketry. Klamath people decoct flowers, leaves, and stems for a head and facial wash for girls' puberty customs.

Invoking Darwin's observations on the specificity of plant-pollinator associations, I return to the mutualistic relationship between the cochineal insect and *Opuntia* cactus. Cochineal is used medicinally for both its activity and the red color that in particular cultural contexts signals potency, efficacy in treating blood disorders, and heightened cognitive function. It enhances IgM production, prevents carcinogen-induced DNA damage in experimental animals, and is antithrombotic, antibacterial, estrogenic, and immunomodulatory (Etkin 2006: appendix, Kuramoto *et al*. 1996, Takahashi *et al*. 2001). Carminic acid is the basis of carmine which has been used to color a wide range of manufactured goods (textiles, cosmetics), including foods (yogurt, juice) and pharmaceuticals.

Cochineal dye has a rich history in Central and South America. It was used by Aztec and Maya for body decoration, food, textiles, and tribute. It became Mexico's most valuable export, second only to silver. During European expansions, large-scale production was developed in the Canary Islands, Central America, and Guatemala. By the late 1700s, it was such an important item of global commerce that its price was quoted on the Amsterdam and London Exchanges. Its use for dye began to decline early in the twentieth century in a trajectory whose mirror image is the advent of aniline dyes; but in the last decade, its culinary uses have been expanding in response to concerns about artificial food additives (Novak 2008, Portillo & Vigueras 2008).

The most commonly reported traditional uses of *Opuntia* species are the application of stem ash and cladodes to burns and wounds, both for healing and analgesia, and to treat mucous membrane irritation, including ulcer. Cut stems treat snake bite. Small thorns are applied with pressure to warts to remove them, and to pierce boils. Crushed pads are used topically for backache. Dry stem pith is applied to ear infections and other otic disorders. Some *Opuntia* species are purgative, others are consumed for diarrhea and other gastrointestinal disorders, for example *O. tunicata* Link & Otto in Hawai'i (Yarnell *et al*. 2003).

A broad range of therapeutic action characterizes the genus *Opuntia* and represents both experimental models and supplementation of human and animal diets. Topical application of cladode polysaccharides promotes cutaneous repair through re-epithelization and remodeling phases. Better outcome with the lower-molecular weight polysaccharides invites the speculation that the more delicate structure of these compounds imparts more effective rheologic, viscoelastic, and hygroscopic activity (Trombetta *et al*. 2003). Some species are active against tumors and demonstrate antiviral, antidiabetic, and trypanocidal effects. The cholesterol-lowering action is attributed to pectin and other soluble fibers, and has been observed in experimental diets that include seed. The fruit juice contains many phenol compounds and is hepatoprotective. Mucilages demonstrate cytoprotective effects on gastric mucosa (Ennouri *et al*. 2006, Fernandez *et al*. 1994, Galatie *et al*. 2005, Galatie *et al*. 2007, Mtambo *et al*. 1999, Tesoriere *et al*. 2004, Trejo-Gonzalez *et al*. 1996, Valente *et al*. 2007).

Wherever *Opuntia* grows, virtually all plant parts are identified as food: flowers, calyces, berries, seeds, stems, joints, and pads. Thorns are always removed, otherwise preparations vary, including drying for storage as a staple, cooking or eating fresh, and preparing fermented beverages. Throughout its region of origin and the U.S. Southwest, the range of prickly pear foods is especially broad. In the Mediterranean, cactus fruit, cladodes, and young stem segments are popular foods; wines and liqueurs are made from the fruit of some species (Yarnell *et al*. 2003).

Insect-Trapping Plants

The historical, unattributed observations in the following discussion are drawn from a several-page summary by Juniper and colleagues (1989). References to Native American uses of trap plants are attributed to Moerman (1998); Hartwell (1982) is credited with observations about the use of trap plants for tumors and cysts.

As noted above, virtually all trap plants have acid phosphatases, esterase, and protease. The hairs and glands of some species release chitinase, which is antifungal. Other digestive enzymes that are unevenly produced by trap plants are peroxidases, lipases, glycosylases, and ribonucleases. Antimicrobial and anticancer phenolics present in trap plants include quercetin, droserone, kaempferol, shinianolone, isoshinanolone, and epishinanolone. Kaempferol is a strong antioxidant that has antiatherosclerotic activity, including platelet inhibition. It acts synergistically with quercetin to suppress cancer cell proliferation. Many, including all *Drosera* and most *Nepenthes*, produce naphthoquinones such as plumbagin, which is broadly antimicrobial against tuberculosis, *Bordatella*, bronchial infections, and Hansen's disease; antimalarial; antispadmodic; antiasthma; granulocyte-enhancing; anticancer; abortifacient; antiatherosclerotic; cardiotonic; and immunomodulatory; and has antifertility action. *Nepenthes* proteinases include nepenthesins I and II which, among other activities, inhibit bacterial growth in the pitcher. Common pigments across this group of plants are anthocyanins, which have antitumor activity. Aucubin has hepatoprotective activity (Aung *et al*. 2002, Hatano & Hamada 2008, Jayaram & Prasad 2005, Kolodzie *et al*. 2002, Schlauer *et al*. 2005, Sharma *et al*. 2007, Suh *et al*. 1991).

Sarracenia plants and extracts are used by Native North Americans for a broad spectrum of disorders as a diuretic, and for pain and fever. Preventive and therapeutic applications for infections include urinary, gynecological, and intestinal disorders; *Bordatella*, smallpox, pneumonia, and tuberculosis infections. Extracts are active against leukemia and human epidermal carcinoma, which might be attributed to betulin or sarracenin. Combinations of coniine, amines, and volatile compounds are toxic. *S. purpurea* triterpines and phytosterols appear in commercial "herbal" preparations. Essential oils of *S. flava* L. contain the antifungal sesquiterpene caryophyllene, the antibacterial ß-pinene, and the triterpene betulin which is anti-inflammatory, antiviral, and tumor suppressive. Lupeol, another triterpene induces apoptotic cell death in pancreatic cancer and inhibits aggressive human metastatic melanoma (Green *et al*. 2007, Jaffe *et al*. 1995, Saleem *et al*. 2008). Trap secretions have been observed to anesthesize flies (Schnell 2002).

Sarapin is a commercial alkaline suspension of *S. purpurea* leaves that is based on a traditional pain treatment and used as a trigger point injection to treat neuralgia. Clinical studies in the mid-1900s suggested that Sarapin was effective in mediating pain associated with neural blocks. These findings have not been corroborated by other studies, including a prospective double-blind trial with a large patient population who served as their own controls (Manchikanti *et al*. 2004).

In Malaysia, the powdered root of *Nepenthes* is used to treat gastrointestinal disorders, which might benefit from the presence of naphthoquinones, the activities of which are discussed above. The plant is astringent and emetic, a stem infusion treats fevers. The pitchers are part of the material culture of rites of spirit exorcism and encouraging rain. The vines are used for cordage (Burkill 1966, Lloyd 1942). In Malaysia, a decoction of *N. ampullaria* Jack root is drunk to treat stomachache and dysentery (Wiart 2006). Fluids from unopened traps have been used as laxatives and to treat burns and skin disorders. In the Philippines, traps are used to transport water, as drinking cups and, purportedly, as cooking vessels (Pietropaolo & Pietropaolo 1986: 40).

The leaves of *Pinguicula vulgaris* L. are used to treat sores in veterinary and human medicine. Macerated in wine, the same leaves are indicated for edema; in sugar syrup they are taken for diuretic and purgative action. Well into the second half of the twentieth century in rural Europe, milk was coagulated through the addition of butterwort sap and leaves, or feeding the plant to animals prior to milking. The mucilage alone has the same effect (Lloyd 1942). The process is not marked by whey production, which suggests something in addition to casein modification, and may involve bacteria associated with the leaf surface or secretory glands. Extracts of *P. vulgaris* are antispasmodic and bactericidal; diuresis might be attributed to the presence of quercetin and other flavones.

Drosera anglica Huds. and *D. intermedia* Hayne are European medicines for spasms and cough. Other *Drosera* species are used for cough and cardiac disorders and, on the strength of their reputation as aphrodisiacs, in the production of several liqueurs, in Austria in the preparation of sweet pastries, and in Australia as a sweetener. In the United States, a tincture of the leaves is used to treat atherosclerosis and to decelerate aging. Caustic liquid pressed from fresh leaves treats warts, corns, cysts, sunburn, bunions, and freckles. The sticky leaves serve as an amulet to attract a woman's attention. Native peoples representing diverse geographies use the dry leaves of *D. peltata* Sm. ex Willd. to treat dental caries (Didry *et al*. 1998). Other species are used for *Bordatella* cough and other bronchial infections, which could benefit from its antispasmodic and broad spectrum antimicrobial action. Antitussive activity also has been established. *Drosera burmannii* Vahl treats dysentery and malaria in China, and spasms and *Bordatella* in Cambodia, Vietnam, and Laos. In Cambodia and Vietnam, *D. indica* L. is applied to patches of thickened skin (Schilcher & Elzer 1993, Wiart 2006). In the United States and Europe, the secretions of *D. indica*, *D. longifolia* L., and *D. rotundifolia* are applied to tumors and cysts. *Drosera indica* occurs in diverse African pharmacopoeias to relieve pain and treat skin infections (Iwu 1993).

Conclusion

This ethnobotanical study focuses on Darwin's plants, selecting from the thousands of taxa that he examined to describe plants that I positioned as two ends of a spectrum of fascination, but that, for different reasons, captivated Darwin in equal measure. The intention is not to compare these two groups of plants, but to use the descriptive terms "insect-trapping" and "common garden varieties" to identify taxa for ethnobotanical inquiry. The botanical descriptions resonate a suite of themes that framed Darwin's work: plant reproduction, flower morphology, pollination, flower-pollinator specificity and co-evolution, cross-fertilization, varieties and speciation, and movement. Casting the same plants in a biocultural perspective allows us to speculate on the intersection of the cultural construction and social negotiation of these plants with their tangible features – appearance and apparency, pharmacologic and other activities, and nutrient potential. Several examples are mentioned in the foregoing discussion: plants used to treat wounds, fever, and cough might have antimicrobial properties, or naphthoquinones in *Nepenthes* species might benefit gastrointestinal disorders. This approach has proved fruitful for the disciplines that contribute to the overlapping perspectives of ethnobotany, anthropology and ethnography, ethnobiology, and ethnopharmacology. In general, many of the tangible aspects of these and Darwin's other species match the medicinal, culinary, and symbolic uses of these plants. At this juncture, the juxtapositions of phytochemical activity and use are speculative, but they allow us to develop hypotheses that can be tested in specific ethnographic, laboratory, and clinical settings.

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