NECTAR; WHAT IT IS, AND SOME OF ITS USES.*

[As the investigation of cotton insects has progressed, the importance of the nectar glands of cotton in their influence upon the natural enemies of the cotton and boll worms, has gradually become more and more apparent, until at last it seemed imperative that some space should be devoted in the report to a consideration of the general subject of nectar. The following chapter was, therefore, prepared, at my request, by Mr. William Trelease, who has made the subject of the mutual relations of plants and insects a special study.—J. H. C.]

Though as a scientific word it should possess precision, the word nectar is far from conveying one idea when met with in the writings of different authors. Purely mythological with most of the Greek and Roman writers, it signified the beverage of the gods. By Virgil it was used apparently much as we now use it. "Others [of the bees] compress the clearest honey, and swell out the cells with liquid nectar."†

Linnæus defined a nectary as a "*pars mellifera flori propria*," whence nectar is a honey-like substance produced by such a floral gland. Dr. Gray defines the word as follows: "Nectar: the honey, &c., secreted by glands or by any part of the corolla";‡ or, again, "Nectar: the sweetish secretions by various parts of the blossom, from which bees make honey."§ Sachs says, "Glandular organs are found in the flowers which secrete odorous and sapid (generally sweet) juices, or contain them within their delicate cellular tissue, from which they are easily sucked

* Since nectar is found in several parts of the cotton plant, and presents some peculiar phenomena there, it has been thought best that I should treat briefly in this place of its occurrence and economic value; hence the present essay. My plan has been to indicate what I understand by the word nectar; to describe some of the more instructive instances of its occurrence, in an order depending entirely upon the nectariferous organs; to then arrange these according to the purpose which the nectar serves in each case; to discuss some of the cases more at length; and, finally, to briefly mention the habits of some nectar-loving animals when in quest of this beverage. Though limited time and prolonged ill-health have prevented me from making this essay what I had wished it to be, I trust that it may not be found wanting in what it professes to be—an outline of the uses of nectar as we now understand them.

WM. TRELEASE.

Ithaca, N. Y., *November* 12, 1879.

† Georgics, iv, l. 164.

‡ Lessons in Botany, 1868, p. 222.

§ Structural Botany, 1879, p. 421.

out. These juices are included under the term nectar."* Delpino proposes to replace the Linnæan definition of a nectary by the following: "*Pars mellifera plantarum angiospermarum propria*";† whence nectar is a honey-like fluid produced by such glands situated anywhere on an angiospermous plant. This not only excludes honey-dew, which Delpino regards as a pathological symptom, but also the nectar which Francis Darwin has found secreted by true glands on *Pteris aquilina*, a fern. Darwin‡ discusses the case of some Orchid flowers which contain a sweet fluid between the walls of their nectaries, whence it is abstracted by insects after they have pierced these walls. This fluid is spoken of by him as nectar. Reinke defines nectar as "a clear fluid of sweet taste, elaborated by certain aerial parts of plants."§

Though the elimination of a sweet fluid (honey-dew) on the leaves of plants may be due to a diseased condition of the leaves in many instances, yet as it is of frequent occurrence, and as the nectar in the last case mentioned is not elaborated by specialized glands, it seems best that this should also be included in a definition of nectar. The following definition is, therefore, proposed in the belief that it comprehends all of importance that any previous definition has included, and nothing—save the honey-dew, just mentioned—not included by some good authority. NECTAR: a fluid always sapid, usually sweet, often odorous, which is elaborated in any part of a plant, remaining where formed or making its way to some other part; its *raison d'être* being the necessity for the removal of some useless or injurious substance, or for some provision to attract nectar-loving animals to the plant for some definite purpose.

It has long been known that specialized organs for the elaboration of nectar—nectar glands—exist in the flowers of many plants as well as outside of the floral envelopes of some. These glands, when occurring outside of the flower, always consist of modified epidermal tissue, as shown by Martinet: they may be said to be made up of an inactive supporting portion, the adenophore of Martinet (Pl. III, Figs. 1, 5, *a*), and of an active superficial portion, the gland proper (Pl. III, Figs. 1–5, *g*). These glandular cells are far different from the epidermal cells of which they are but modifications; thus, in glands from the petiole of the castor-oil plant I found them to be divided by transverse septa; and in the foliar glands of the cotton plant to be marked by coarse reticulations on their walls, making them appear at first sight as though not simple cells. In the latter case, too, their distal portions are quite separate from each other, so that they resemble, to a certain extent, crowded villi. Within the flower, glands may be of varied structure, sometimes superficial, sometimes deep, possessing less uniformity than elsewhere.

According to their situation, these glands may be either floral or extra-floral; the former occurring within the floral envelopes, the latter, without

* Text Book of Botany, English translation, 1875, p. 500.

† Ulteriori Osservazione, 1875, p. 85.

‡ Fertilization of Orchids, 2d edition, pp. 36–44.

§ *Pringsheim's Jahrbücher für wiss. Bot.*, 1875, x 119, note.

them. Floral glands may occur as modifications or appendages of any of the floral organs; extrafloral glands may occur as modifications or appendages of the outer floral envelope, or of various extra floral organs, as shown in the following table:

Floral.....	Receptacle.
	Pistil.
	Stamens.
	Corolla.
	Calyx.
Extrafloral.	Calyx.
	Ordinary bracts.
	Specialized bracts.
	Involucre.
	Peduncle.
	Leaf.

The secretion of glands of the first group seems always designed to aid in the fertilization of the flowers in which it is produced by attracting to them insects or birds, which, by reason of some floral adaptation, while feeding on the nectar, or on small insects likewise attracted to it, unconsciously transfer pollen from the anthers to the stigma of this or some other flower of the same species. Some of these flowers are of an open structure, with their nectar accessible to insects of all sorts and sizes; others are of such size and form as to be limited to certain groups of insects, sometimes even so restricted as genera. Some are so formed that fertilization is possible by direct pollination without extraneous aid; others never produce offspring unless they receive such aid. So much has been written concerning floral nectar and its uses that I shall give but one example under this head, the flower of the cotton plant.

The cotton flower is very fugacious; opening shortly after sunrise, it has passed its prime before sunset, and by the end of the second day the corolla and stamens have usually fallen to the ground.*

*As is well known, the corolla of one of these flowers is creamy white on opening; later in the same day it becomes more or less tinged with pink or rose, which becomes a uniform deep rose on the second day. As will presently be shown, these flowers are not dependent on insect aid for their fertilization, yet the great size and conspicuous color of their corolla indicates to the believer in the commonly accepted theory of the evolution of floral forms that this has not always been the case; in other words, that there was a time when, for some purpose, they needed to attract insects or other animals, to which their showy corollas rendered them visible from a distance. But why should the color change so markedly as the flower advances in age? There is reason for believing that fertilization occurs during the first day of blooming, and this being the case insects are not needed by any flower more than one day old. Many other cases could be given where the color of a corolla changes and becomes intensified after the fertilization of the flower to which it belongs, but it is unnecessary to more than mention them here. The most satisfactory explanation of this phenomenon that is known to me is that by their varied, lasting, and augmented coloration they attract flower-haunting animals to the plant. These instinctively, or by experience, visit only the younger flowers, readily distinguishable by their color from the older ones. See Nature, ix, 460, 484; x, 5; xvii, 78; and Delpino, Ult. Oss., 1875, p. 28.

The reproductive organs are so placed that on the expansion of the corolla pollen has usually been deposited on the stigmas, self-fertilization being thus secured. By his many observations and experiments, Darwin has shown that where self-fertilization is thus provided for, occasional crossing is often of sufficient importance to warrant the production of large and conspicuous corollas, and of nectar accompanied by fragrance to secure such crossing by inducing suitable animals to go from flower to flower. Such appears to have been the case here, for within the corolla, where the petals separate from one another and from the staminal column, is found a set of small hairs which are slightly viscid as shown by the adhesion of pollen grains to them. What causes this viscidity? Early in July I noticed a single hive bee within a cotton flower, where, as I then supposed, it had gone to collect pollen, but I failed to see that it did. About the same time I saw many humble-bees entering the flowers for pollen as I thought, and they, too, went unnoticed, though they transferred much pollen from flower to flower in these visits. Shortly afterward I noticed certain sand-wasps belonging to the genus *Elis* within the flowers, and as I did not know that they fed on pollen I was led to watch their actions. Instead of collecting this substance they were exploring with their tongues the clefts between the petals; this led me to examine a flower more closely, the result being the finding of the hairs just mentioned. As no nectar was found elsewhere in the flowers, and as these insects were constant in their visits, I infer that viscidity of the hairs is caused by an exudation of true nectar.* Darwin describes a similar secretion from hairs on the labellum of *Cypripedium*.†

Numbers of specimens of the beetle *Chauliognathus marginatus* were found within the flowers, where, however, they ate only pollen, so far as I could see. Individuals of the yellow butterfly *Callidryas eubule* were often seen resting on the free border of the petals and sipping the nectar with their long and flexible proboscides. The following-named insects were all seen in greater or less numbers in the flowers after nectar: *Elis 4-notata*, *Elis plumipes*, *Melissodes nigra*, *Megachile sp.*, and *Bombus sp.*

In thus collecting pollen and nectar, these insects, with the exception of the butterfly, coming in contact with both anthers and stigmas, became well dusted with pollen, which necessarily was transferred in quantity from flower to flower. The species most frequently met with in these flowers were *Elis plumipes* ♂ and *Melissodes nigra*.

As an example of extrafloral nectar produced on the calyx, I shall cite that of the leguminous plant, *Coronilla varia*, described by Farrer.‡

* In the Popular Science Review for July, 1869, p. 270, Ogle states that, as previously noticed by Vaucher, no nectaries are found in Synœnic Malvaceæ. This appears to be an exception to that rule, for, so far as I could see, the stigmas were perfectly receptive when the corolla expanded.

† Fertilization of Orchids, second edition, p. 229.

‡ Nature, x, 1874, p. 169.

Here the outer surface of the calyx is covered with small glands, the secretion of which attracts bees to the flower; but, strangely enough, instead of alighting directly on the calyx and lapping up the nectar, they settle on the wings and keel, whence they protrude their tongues back into the flower and out between the separated bases of the petals, thus indirectly reaching the nectar on the calyx. Despite their usual intelligence, we are led to the conclusion that in this case the bees are deceived, believing the nectar to be within the flower, as is the case in so many of the Leguminosæ, instead of on its exterior. But this deception, if deception it be, is of value to the plant, for in resting on the wings and keel the bees depress these petals, bringing their breasts in contact with stigma and pollen, and effecting the cross-fertilization of different flowers, in their visits from plant to plant.

Another example is afforded by the cucurbitaceous plant cultivated in the South, under the name of bonnet-squash or dish-rag plant. Each lobe of the calyx has on its outer side a varying number of glands, which secrete nectar for some time before the flower opens during the period of blooming, and for some time after fecundation has occurred. This nectar is so greedily sought by ants of several species that numbers of them are to be found at all times on every calyx which is in active secretion, but they seldom enter the flower, apparently being prevented from doing so by the large, spreading corolla.

The common passion-flower or May-pop of the South (*Passiflora incarnata*) affords a good illustration of nectar occurring on small, unmodified bracts. At the base of every flower are found three or four small bracts, each bearing two large nectar glands. Though the secretion of these is not very plentiful, it is sufficiently so to attract swarms of ants, which, as in the last case, do not enter the flowers, apparently finding the spreading sepals and petals and the dense corona insurmountable obstacles.

In the tropical *Marcgravia nepenthoides* (Pl. III, Fig. 6), Belt tells us that "the flowers are disposed in a circle, hanging downwards, like an inverted candelabrum. From the center of the circle of flowers is suspended a number of pitcher-like vessels, which, when the flowers expand, in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds. The flowers are so disposed, with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another."* These pitcher-like vessels are modified leaves or bracts, the nectar of each gland being secreted inside a sort of pouch, and passing to the surface through two pores or ducts.†

Good examples of nectar borne on bracts collected into an involucre are afforded by some of the Euphorbias. Thus in E. (*Poinsettia*) *pul-*

*Naturalist in Nicaragua, 1874, p. 128.

†For the structure of these glands see Wittmack, *Botanische Zeitung*, No. 35, Aug., 1879, s. 557.

cherrima (Pl. III, Figs. 7–10), the flowers are collected into clusters consisting of a central, stalked, pistillate flower, surrounded by a varying number of stalked monandrous staminate flowers, the whole cluster being inclosed in an involucre so as to resemble somewhat a single flower. On the side of each involucre is a large, yellowish, cup-shaped gland, which secretes a considerable quantity of nectar during the blooming period of the cluster to which it belongs. In the house this is sought by myriads of the small red ant *Myrmica molesta*, and in the open air of its native place probably by small bees and flies such as are known to visit other Euphorbias. When one of these clusters begins to expand the pistillate flower at its center is protruded (Pl. III, Fig. 8, *o*), and expands its three bilobed stigmas, which are ready for fecundation. A few days later, these having withered, the stalk of the pistillate flower becomes sufficiently elongated to protrude the entire ovary* (Pl. III, Fig. 7, *o*), and by this time several of the stamens have become exserted and shed their pollen. From this it appears that in this species self-fertilization is impossible, since there are no perfect flowers; the first remove from this, crossing between flowers of the same cluster, is likewise impossible, owing to the maturing of the pistillate flower before any of the staminate flowers are mature; and the closest cross that can occur is between different clusters on the same plant, which, as appears from the crowded structure of these clusters, is about equivalent to crossing different flowers on the same plant of such a species as the Marcgravia figured, for a number of these involucrate clusters are collected together and surrounded by a whorl of bright crimson bracts, rendering the whole very conspicuous to such insects as are in search of nectar. These insects, in obtaining the nectar, necessarily brush the floral organs and must secure the cross-fertilization of the species.

Another example of nectar borne on a floral involucre is afforded by the cotton plant, where each flower is surrounded by a whorl of three large laciniate bracts, on the outside of each of which, near its base, is a nectariferous pit.†

Alternating with these bracts, and just within the circle formed by their bases, are three other pits, smaller than the former, but like them, active.‡

The first few flowers that open possess only rudiments of glands; but

* In cultivation the pistillate flower is often entirely abortive (Figs. 9 and 10), and its ovules seem to be always aborted in our greenhouses, for though an abundance of apparently good pollen is produced I cannot learn that the species ever set seed with us. My authority for this failure to set seed is Peter Henderson, the well-known New York florist. See Gray, Silliman's Journal, 3d series, xiii, 1877, p. 138; and some notes by myself, Bulletin Torry Botanical Club, vi, 1879, p. 344.

† Glover, Agricultural Report, 1855, p. 234, mentions these glands, as well as the inner set and their secretion of a "sweet substance, which ants, bees, wasps, and plant-bugs avail themselves of as food."

‡ These glands belong, in reality, to an inner whorl of three bracts, alternating with the outer ones, but generally wanting. In stunted plants, especially as cold weather comes on, one or more of these inner bracts may often be found. ((Pl. III, Fig. 13.)

all after the first few possess the outer set, though it is not till the cotton has been blooming about a month that the inner set appear. Confining our observations to flowers which possess both sets fully developed, we find that a number of days before a flower-bud opens all of its involucral glands are visited more or less frequently by ants, and occasionally a wasp or hive bee may be seen about them, although to our eyes they are dry. Evidently, then, they secrete a thin sugary film. The evening before such a bud opens, its visitors increase in number, and we may, perhaps, see a little nectar in its glands. But during the night preceding its unfolding, its cups fill out with the sweet fluid which is collected by large numbers of ants, and early the next morning a large drop may be seen suspended from the lower margin of each, or in some cases running down the bract; and throughout this, which may be called *the* day of blooming, bees, wasps, and ants of many species may be found in constant attendance on the glands. Though drawn so close to the flowers, these insects never enter them, so they can have no direct influence on their fertilization. Perhaps the strangest thing about these glands is, that during the night, when this abundance of nectar is collecting, they are visited by thousands of the moths of *Aletia argillacea* and *Heliothis armigera* whenever these moths are flying and laying their eggs. This appears to be a strange paradox. Nectar is secreted apparently to attract insects to a plant; and some of the insects so attracted have the instinct to oviposit on the plant, on the foliage, flowers, and fruit of which their larvae feed. How could this secretion have been acquired by natural selection? It looks as if such an acquisition must imply the survival of the unfittest! As has been shown elsewhere, the flowers of the cotton plant suffer from the attacks of the larvae of both these moths; but most of the eggs of both species are laid on other parts of the plant than the flowers or floral appendages, consequently a larva to reach the flower must ascend the peduncle, and run the gauntlet of ants, wasps, and bees found at its summit; though I never saw one ascending when these insects were at their post, and therefore never had an opportunity to see what would happen then. I found that when these larvae are on the leaves of the plant they are sometimes attacked and killed by the ants without any provocation. So it appears that the secretion of these glands first attracts the worst enemies of the plant, and then attracts their enemies, which afford it partial relief from the misfortune that it has brought on itself.

An example of nectar secreted on the flower-stalk is found in the cow-pea. At the summit of each peduncle are several small, crater-shaped, circumvallate glands, which secrete until the fruit is well advanced toward maturity, as well as during the flowering period. Occupying, as they do, the very end of the peduncle, they are beyond the clustered flowers and seed-vessels. In Alabama I found that they are much frequented by ants of several species. Like the cotton plant, the cow-pea is visited by the moths of both *Aletia* and *Heliothis*, but only the latter

oviposits on it, and this in but small numbers, its larvae feeding on the green seeds. The same complication, therefore, exists here as in the case of the cotton plant; but in this case the attack appears to be limited to the early fruiting period, and a body-guard of ants is maintained during this period.

Coming, now, to leaves, we may briefly refer to the sweet fluid known as honey-dew, which is sometimes found on the foliage of plants. In many cases this will be found not to originate in the leaves, but to drip from the anal tubes of *aphides*, or plant-lice; and with this we have nothing to do, since it is not a production of the plant. But in some cases this substance is an excretion from the leaves, apparently due either to the climatic conditions obtaining at the time of its production or to a diseased state of the plant. It is not, so far as I know, produced by structures, such as glands, in any case. Though bees and ants collect this substance with avidity, it does not appear that they render the plant any service while doing so.*

Small glands are found at the tips of the serrations on the leaves of many plants, and some of these produce a plentiful supply of nectar; some of them being frequently visited by insects, and others scarcely at all. Like the last, this nectar is believed by Darwin to be merely excretory, and as going to show that such is the case we may mention the fact that the leaves of peaches, nectarines, and apricots—which may be glandular in some, and not glandular in others of the offspring of a single parent—if glandular, are less liable to the attacks of mildew than if they bear no glands.†

Leighton found that—

> On the upper edge of the vertical phyllodia of *Acacia magnifica*, subtending the showy spikes of yellow flowers, which proceed from their axils, appeared a pellucid drop of liquid, varying in size from that of a large pin's head to that of a grain of mustard-seed. This to the taste was sweet and sugary. The flowers themselves had no odor, except toward nightfall, when they gave out a weak disagreeable smell, only perceptible on close contact. In wiping off the sugary secretion it was observed that it proceeded from a small sunken linear-oblong orifice or slit, surrounded by a swollen margin. * * * The secretion takes place only during the period that the plant is in blossom. So soon as the flowers fade and begin to fall, the secretion ceases and disappears. It would seem then to be in some way or other connected with the fertilization of the flower; and as, when the secretion becomes excessive, it falls and blotches the lateral expansion of the phyllodium, it is probably to attract insects to effect this, * * * it seems almost evident that it would require an insect of some considerable size and of some peculiar structure to remove and apply the pollen, the secretion not being in the blossom itself, but at a short distance from it, on the phyllodium.‡

This case appears quite similar to that of the cotton flower previously given, and I cannot avoid the conclusion that the real object of the nec-

* Darwin, Cross and Self Fertilization, 1877, page 402, mentions undoubted cases of the occurrence of this excretion, besides giving references to other writings bearing on this point.

† For references on this subject see Darwin, Animals and Plants under Domestication, Orange Judd edition, 1868, i, 413: ii, 280.

‡ Annals of Natural History, third series, xvi, 1865, page 12.

tar was to secure protection to the flowers, rather than to secure their fertilization, though the latter might occasionally occur incidentally.

On the lower surface of the leaf of the cotton plant, not far from its base, the mid-rib bears a large sunken nectar gland, and each of the lateral veins of the larger leaves bears a similar gland.* Traces of these glands may sometimes be found on the cotyledons, but I never saw a perfect gland on a seed-leaf. As shown by the visits of ants, the gland of the first leaf begins to secrete when the seedling plant has about four leaves expanded; but it is not till some days later that enough nectar is produced to be noticeable, and from this time on the gland secretes abundantly until the leaf becomes old or diseased. When a gland is in vigorous secretion it may be examined at almost any time of the day, and barely enough fluid will be found in it to fill the pit two-thirds full; but during the night, and until some time after sunrise in the morning, great drops of the sweet fluid may be found hanging from its border. This nectar is very attractive to certain insects, chiefly ants, wasps, and mud-daubers. It is also sought at night by the moths of both *Aletia* and *Heliothis*, the former of which had been seen to alternate sipping this nectar with ovipositing. As I have elsewhere stated, the larvæ of both these moths feed on the leaves of this plant, and both have been attacked, removed from the plant, and killed before my eyes by ants or wasps induced by this nectar to visit the leaves.

On the lamina of the leaves of the bonnet squash a variable number of pustule-like glands is found. These secrete an abundance of nectar, and are constantly attended by ants of several species, which, from the distribution of the glands, are led to explore every inch of the leaf-surface. I only found that the leaves of this plant were attacked by the larvae and imagines of the large lady-bird, *Epilachna borealis*, and as very few of these were seen on them I could not determine their relations with the ants.

In *Acacia sphærocephala*, the bull's-horn thorn, Mr. Belt tells us that—

> The leaves are bipinnate. At the base of each pair of leaflets, on the mid-rib, is a crater-formed gland, which, when the leaves are young, secretes a honey-like liquid. Of this the ants are very fond, and they are constantly running about from one gland to another to sip up the honey as it is secreted. But this is not all; there is a still more wonderful provision of solid food. At the end of each of the small divisions of the compound leaflet there is, when the leaf first unfolds, a little yellow fruit-like body united by a point at its base to the end of the pinnule. Examined through a microscope, this little appendage looks like a golden pear. When the leaf first unfolds, the little pears are not quite ripe, and the ants are continually employed going from one to another examining them. When an ant finds one sufficiently advanced, it bites the small point of attachment; then, bending down the fruit-like body, it breaks it off and bears it away in triumph to the nest. All the fruit-like bodies do not ripen at once, but successively, so that the ants are kept about the young leaf for some time after it unfolds. Thus the young leaf is always guarded by the ants, and no caterpillar or larger animal could attempt to injure them without being attacked by the little warriors.

* Glover, Agricultural Report, 1855, p. —, points out the presence and secretion of these glands.

This Acacia bears large paired thorns, which, when young, are filled with a sweetish pulp. Boring a hole through the wall of one of these young thorns the ants eat out the contents of this one and its mate, this action causing an enlargement of the thorn, so that a capacious chamber is formed, and in this the ants live, remaining constantly on the tree, so that Mr. Belt remarks—

> I think these facts show that the ants are really kept by the Acacia as a standing army, to protect its leaves from the attacks of herbivorous mammals and insects. * * * I sowed the seeds of the Acacia in my garden, and reared some young plants. Ants of many kinds were numerous, but none of them took to the thorns for shelter nor the glands and fruit-like bodies for food; for, as I have already mentioned, the species that attend on the thorns are not found in the forest. The leaf-cutting ants attacked the young plants and defoliated them; but I have never seen any of the trees out on the savannahs that are guarded by the *Pseudomyrma* touched by them, and have no doubt the Acacia is protected from them by its little warriors. *

At the base of the petioles in the greater coffee-weed of the South (*Cassia occidentalis*) are globular glands, which secrete a sufficient quantity of nectar to render them attractive to numerous ants, wasps, and bees, which would be encountered by any wingless insect in ascending the stem or passing out on any leaf. Most of the upper leaves subtending the racemes of flowers are reduced to mere bracts, which, however, have their glands large and active; and these bear the same relation to the flowers and young fruit that those lower down do to the leaves.

Several species of *Sarracenia* (pitcher-plants, or trumpets) have the lids or mouths of their pitcher-like leaves provided with a sweetish secretion which, at certain times, in at least one species (*S. variolaris*), extends along the margin of the wing in front of the leaf so as nearly or quite to reach the ground. Thus a line of nectar runs from the ground to and within the mouth of the pitcher, which is here provided with a fine velvety pubescence, the hairs pointing downward. Just below this is a rough portion, lined with stiff bristles which also point downward. The lower part of the tube, destitute of these hairs, is filled by a watery liquid, wholly or in great part secreted by the walls of the pitcher, and usually protected from dilution with rain-water by the overarching lid of the pitcher, the real blade of the leaf. An insect, lured up the wing and to the mouth of the pitcher, while feeding on the repast so generously offered, slips on the velvety surface, tries in vain to catch a firmer hold, slips farther, and falls into the pitcher, whence the stiff *chevaux-de-frise* makes his escape very difficult. Reaching the water he is sooner or later drowned, and being macerated there contributes to the food of the plant.†

The related *Darlingtonia californica* has a somewhat similarly shaped leaf. Its long, twisted tube is arched above, so as to prevent the access of rain-water to the secretion which fills its lower part, and the part answering to the hood of Sarracenia or the blade of an ordinary leaf is

* The Naturalist in Nicaragua, 1874, p. 219.

† See J. H. Mellichamp's "Notes on Sarracenia variolaris," Proc. Am. As. Adv. Sc., xxiii, 1874, Nat. Hist., p. 113; also Riley, *ibid.*, p. 18; and Trans. St. Louis Acad., iii, 235.

produced in front of its mouth in the form of a fish or swallow tail. As in the last case, the edge of the border of the wing, the mouth, and the blade or fish-tail appendage are provided with a secretion of nectar, as is also the inside of its arched hood; so that insects are attracted as before by the sweets, only to meet their death on entering the tube. The nectar leading from the ground appears designed to attract creeping insects, such as the ants, which form a large part of the prey of Sarracenias, while the swallow-tail appendage appears to be for the purpose of attracting flying insects.*

Like the preceding, the climbing Indian pitcher-plants (*Nepenthes*) secrete nectar about the mouths and on the lids of their cups, and for the same purpose, for they, too, are insectivorous, and, indeed, more truly so than either of the genera previously mentioned, inasmuch as their secretion has been shown to be a true digestive fluid, while that of the others is scarcely demonstrated as yet to be more than a liquid in which maceration may go on.

When the foregoing examples are considered, it appears at once that all nectar may be divided into two classes, according as its relations to the secreting plant are direct or indirect, according as it merely relieves the plant of a waste or injurious substance, or serves to establish definite relations between it and other living beings. Furthermore, the first class is entirely excretory, and is produced either by the unmodified leaf tissues or by specialized glands; the second class is never excretory, and may be subdivided into two groups—as has been done by Delpino—the first aiding in reproduction, and being either intra or extra floral; the second taking no direct part in reproduction, being always extra-floral, and serving indirectly either for the protection of some part of the plant or for its nutrition by attracting animals which, in the one instance, serve as a body-guard to the tender foliage and flowers, and in the other are killed, their remains undergoing decomposition or even digestion in the leaf cavities of the plant, and serving in either case as food for it. This arrangement may be expressed in tabular form as below:

- Directly useful
  - Excretory
    - From the surface.
    - From glands.
- Indirectly useful
  - Reproductive
    - Floral
      - Borne on Sepals.
      - Borne on Petals.
      - Borne on Stamens.
      - Borne on Pistils.
      - Borne on Receptacle.
    - Extrafloral
      - Borne on Calyx.
      - Borne on Bracts.
      - Borne on Involucre.
  - Non-reproductive
    - Protective
      - To flowers.
      - To fruit.
      - To foliage.
    - Nutritive — By securing material for absorption by leaves.

* See Canby, Proc. Am. As. Adv. Sc., xxiii, 1874, Nat. Hist., p. 64.

In order that the significance of some of the examples given may be fully understood it will be necessary to speak briefly of the habits of a few insects. Ants, the most numerous of all the visitors of extrafloral nectar glands, are of various habits. So far as I know all of the species with which I had to do in Alabama are omnivorous, eating nectar and other sweet substances, but largely feeding upon animal food. In pleasant weather they may be found abroad night and day. But this is not true of all ants. The leaf-cutting and umbrella ants, or Saüba of Central and South America (*Oecodoma*), are entirely herbivorous. Excavating large tunnels, and living in immense communities, they are the terror of gardeners in the hotter parts of our continent; for they have the habit of marching in great armies which swarm over and defoliate every unprotected plant, preferring cultivated plants, since they, as a rule, neither possess properties rendering them unpleasant to the taste of the ants, nor special provisions to secure a body-guard of protecting insects, and one or the other of these means of defense is usually found in native plants. Having reached the leaves or petals each ant snips out as large a piece as he can carry and makes off with it to the nest. In damp, warm weather these ants forage at all hours, but when the air is hot and dry they seem to realize that the leaves would dry up and become useless before they could get them to the nest, and so they hunt only during the cooler hours of the day and at night.* Moggridge found that a graminivorous ant of the south of France (*Pheidole megacephala*) works mostly at night,† while McCook finds that the parasol-ants of Texas forage only at night, visiting, then, the tops of the highest trees in their leaf-collecting labor.‡ So great a pest are these ants in Central America that it is found impossible, except by the most strenuous exertions, to cultivate any but native plants.

From this it appears that any plant not protected by an unpleasant principle in its flowers and foliage is very liable to extinction where these ants abound, unless it can secure a body-guard of some kind, and this usually consists of nectar-loving ants. To give perfect protection this force must reside constantly on the plant, finding their food, drink, and lodging, which, it will be remembered, were all found on the Acacia previously mentioned. A less perfect protection would be afforded by ants attracted to the plant for some of their food, but residing elsewhere; but it is probable that so few of them would be on the plant at any given moment that an army of the leaf-cutters would have no difficulty in overrunning it in their sudden onslaught. Let us suppose a case in which the attacking ants travel in small bands and only by night; then, evidently, a good protection would be afforded by a small number of pugnacious, nectar-loving ants, called to the plant chiefly or

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* See, on these ants, Bates, Naturalist on the Amazons, and Belt, Naturalist in Nicaragua.

† Ann. Nat. Hist., series —, xiv, 1874, p. 92.

‡ Quoted by Bettany, Nature, Oct. 16, 1879, p. 583.

solely at night. In this case the plant would be under the necessity of secreting nectar only during the night.

As I have stated before, the extrafloral nectar of the cotton plant is far more abundant during the night and in the early morning than at any other time, and this is true whether we consider the involucral or foliar glands. At first, from the visits of ants to glands in which I could detect no nectar, and from the fact that when the largest drops of nectar were seen early in the morning, the leaves were covered with dew; I was led, after satisfying myself that these drops were not confluent dew-drops, to conclude that a thin film of saccharine matter covers the glands at all times when they are in a healthy condition and of sufficient age, and that this is hygroscopic, absorbing so much watery vapor from the damp night air as to present the phenomenon mentioned. But I was led to doubt this conclusion by noticing that the secretion of the involucral glands lasts only during the blooming period of the flower about which they are placed, and I could see no reason why their nectar should be hygroscopic for so brief a time. This led me to examine glands in damp weather, before, during, and after a rain; but no drops of nectar were found, though drops of rain-water were occasionally found hanging from the border of the glands. So the hygroscopic theory would not do. On the contrary, I found that in the early morning after a cloudy or rainy day, there was comparatively little nectar in the glands, which seems to show that the secretion during the night is the result of the solar impulse of the preceding day. I could then scarcely avoid the conclusion that this nectar was originally developed by natural selection, that it might attract some nectar-loving animal to protect the plant from the depredations of some leaf and flower eating creature whose visits were chiefly made at night; and such I believe to be the case, both attackers and defenders having been ants in all probability.

But, it may be urged, you have said that this nectar is, at the present time, an important factor in securing the well-being of the plant, since it attracts ants and wasps which are among the most powerful of the natural enemies of its great spoliators, the boll-worm and cotton caterpillar; why can it not have been developed to secure protection against them or some similar insects? The fact that it is protective to the plant in this way is undeniable; but from what we know of the economy of nature it seems improbable that a nocturnal secretion of nectar should have been secured as a means of protection against larvae which feed for the most part by day; while its very abundance at night was certain to greatly increase their number on plants where this peculiar secretion chanced to be most marked during the process of selection, by attracting to those plants a greater number of the moths whose offspring the larvae are.

On the other hand, it may be urged that inasmuch as this nectar is now so attractive to the moths of *Aletia* and *Heliothis*, it probably does more harm to the plant in attracting them where they may lay their

eggs, than good in drawing the enemies of their larvæ; and, this being the case, natural selection ought to remove the power of secretion. But a moment's reflection will show us that natural selection cannot for this reason remove the glands or their activity. For a long time the cotton plant has been subjected to the methodical selection of man, who, in selecting seed to sow, pays no attention to the presence or absence of active nectar glands on the parent plant, but seeks to produce prolific plants of vigorous growth and good staple; so that no peculiarity which does not tend directly to lessen the vital force of the plant, and thus bring itself directly into conflict with the purpose of man's selection, can be removed by natural selection. But if, under the same circumstances, the production of this nectar is a direct drain on the vital force of the plant, a very different result must follow; for the methodical selection of man then becomes a factor in the broader selection of nature, and tends to the extinction of those varieties which, owing to their greater secretion of nectar, were even a little less vigorous or less prolific than their fellows which chanced to secrete less, so that the result must inevitably be the partial or total absence of nectar in the most vigorous and prolific varieties. My observation has shown me that there is not a whit less nectar secreted by the glands on the finest "Dixon-cluster" stalk than by those of the poorest scrub; from which I infer that the production of nectar causes very little drain on the energy of the plant aside from the mere vital force which must preside over every physiological act. This, I think, goes to show the correctness of Darwin's idea that all nectar was at first merely an excretion; and also that the material used in the elaboration of nectar by large, specialized, and active glands which serve other than excretory purposes is of such a nature that it can readily be spared by the plant without any impairment of its vigor.*

But if the glands of the cotton plant seem to have been produced to secure the protection of the leaves and flowers of the plant from leaf or petal eating insects like ants, those of the cow-pea seem designed to protect the flowers and especially the young fruit from all insects, but chiefly from such fruit-eating larvæ as those of *Heliothis*.

While watching *Vicia sativa*, Darwin found that hive bees, while visiting the stipular glands, "never even looked at the flowers which were open at the same time; whilst two species of humble-bees neglected the stipules and visited only the flowers."† About 10 a. m. one day in August, while the sun was shining brightly, I noticed that several humble-bees,

* This, I think, explains the fact that the glands of *Pteris aquilina* still secrete while the frond is young, though they are not needed for its protection against any insect, as discovered by Francis Darwin. They were probably developed centuries ago, when the young fronds may have experienced the most urgent need of protection from some leaf-eating animal, and, causing little drain on the vitality of the plant, are still retained, though in some, perhaps all, parts of the world they are no longer of use.

† Cross and Self Fertilization, 1877, p. 403, note.

flying about a mixed thicket of *Cassia occidentalis* and *C. obtusifolia*, visited only the flowers of the latter. At the same time many hive bees and small wild bees were seen visiting the extrafloral glands of the former, but none visited the flowers, nor were any humble-bees seen to visit either flowers or petioles of this species. On other occasions I saw hive bees, humble-bees, various small bees, wasps, ants, and moths at the petiolar glands of *C. occidentalis*, but not one of these was seen in the flowers of this species; while in the case of *C. obtusifolia*, as before stated, humble-bees were seen to visit the flowers, but not the extrafloral glands, which appear inactive—at least in Central Alabama. I also found that while both the outer and inner involucral glands of the cotton plant were visited, when in active secretion, by hive bees, but one individual was seen to enter a flower; and while humble-bees entered the flowers constantly, but one was found at each set of involucral glands. Humming-birds were often seen about the flowers of cotton, but none were ever seen to insert their bills within the corolla, all confining their visits to the glands about the flower. Their actions are somewhat curious, inasmuch as a given individual visits at any one time only one set of these glands. Thus on two occasions I watched several which went only to the outer set; but on two other occasions several were seen to confine their visits exclusively to the inner set. Not having marked individuals, I could not, of course, determine whether a given bird always limits itself to one set of glands, but I scarcely think that this can be the case.

In brief, then, we see from the examples given that nectar, wherever it occurs, may be considered as excretory, reproductive, protective, or nutritive; that in some cases, *e. g.*, the leaves of the peach, excretory nectar may possibly be protective also; that reproductive nectar usually occurs in the flowers but not always; that protective nectar seems in some cases designed to keep ants from defoliating and deflouring the plant; in others, to keep larvae from destroying the foliage or immature fruit; that nutritive nectar may serve in some cases to lead to the capture of wingless, in others of winged, insects; and finally that the vital force of a plant is taxed so little in the production of nectar that glands once developed and endowed with the power of active secretion may continue to secrete for generations after the necessity for their secretion has ceased to exist.

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