MYRMECOPHILISM.

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[Address of the retiring president of the Cambridge Entomological Club, 11 January 1889.]

It is customary in some circles for a president's address to consist of a general résumé in some line of scientific work. I have availed myself of this opportunity to review the more important literature on a branch of biological work which has long possessed an unusual degree of interest for me,—namely, the mutual relations, amounting in some cases to symbiosis, existing between ants and certain members of the vegetable kingdom. Such a forced review is profitable to the writer, and it may be of interest to the body before which it is read; but it by no means follows that it has scientific value, for each worker must perforce go back to original sources for information needed in his own researches. Quite naturally, I have treated the subject from a botanical standpoint, since, with the exception of certain acquired habits, the specializations are chiefly such as fit plants to profit by the visits of ants to their vegetative or fruiting organs.

1. The functions of extra-nuptial nectar-glands.

The chief sorts of glands situated on the surface of plants or opening superficially, are divided into colleters and nectar-glands, according as they secrete resinous, mucilaginous, or gummy substances in the one case, or sugary fluids in the other. The first are apparently for the most part protective, in that they form a coating over young parts in the bud, which prevents drying or other injury; or they prevent the access of unbidden guests to the flowers or fruit, or deter vegetable feeders from making an onslaught on the parts which bear them, —in this respect resembling raphides, alkaloids, volatile oils, etc., within the plant.* A few such structures serve for the attachment of fruit or seed to animals for purposes of dissemination, etc. The digestive glands of carnivorous plants may, perhaps, be regarded as derived from some of the numerous types of colleters, and the foliar nectar-glands of many plants are pretty clearly homologous with the serration- and other colleters of the same and related species. Typical colleters are, therefore, chiefly protective, and there is good reason for believing that many of them have been evolved for preventing the access of ants to the flowers of plants, where, almost without exception, the presence of these insects works mischief.

Nectar-glands, on the other hand, are of indirect use by attracting suitable pol-

* For a recent discussion of the protection of plants, especially from the attacks of snails, by colleters and other deterrent structures, see an elaborate paper by Stahl in Jenaische Zeitschrift für naturwiss. und medicin, xxii.—reprinted under the title "Pflanzen und schnecken," Jena, 1888.—Abst. in Bot. centralblatt, 1888, v. 36, p. 164-170.

linators to the flowers, by luring prey to the digestive apparatus of some carnivorous plants, or by maintaining upon the plant a body-guard of pugnacious insects, which more or less efficiently protect it against certain of its enemies.

Since the time of Sprengel (29), it has been well known that many flowers contain glands which secrete nectar as a source of attraction to insects able to cross-pollinate them. The occurrence of this fluid was known long before his day, but its use was either not investigated, or misunderstood. Indeed his keen insight into its *raison d'être* was scarcely appreciated for three-quarters of a century, until Mr. Darwin took the subject in hand in his classical work on the pollination of orchids. To-day, however, Sprengel's views, cleared and somewhat broadened, and carried into a thousand little details that he had not followed out, are contested by very few persons. So far as our purpose is concerned, nothing further need be said of floral nectar, since the structure and habits of ants are such as to practically debar them from any important rôle in pollination. In fact entomophilous plants usually teem with devices for preventing their access to floral nectar,—for which, very naturally, they have a great liking.

The relation of extra-floral nectar to the fructification of plants was, I believe, first clearly pointed out by Delpino, (6, 86), who coined the terms "nuptial" and "extra-nuptial" to indicate on the one hand that which attracts pollinators, and on the other, that which is of no value in this respect. These terms are much less objectionable than "asexual" and "sexual," the former of which has recently been used by Kny (13) as synonymous with extra-nuptial. With nuptial nectar secreted outside the flower, we have quite as little to do as with that secreted within it, for the reasons already indicated; but the subject of extra-nuptial nectar and its relation to ants, is deserving of a much fuller discussion than can be given to it here without going into details to a tiresome length.

Without an undue amount of searching, I cannot say when or by whom it was first observed that certain flowers produce nectar outside of their flowers, but it has certainly been known for a long time. Hall, a pupil of Linnaeus, had seen the extra-floral glands of various plants (11, 266). Krünitz (14), whose work I know only from references in Sprengel and elsewhere, observed bees at the stipular nectaries of *Vicia*, over a century ago, and similar observations had undoubtedly been made, if not heeded, even earlier. But the first careful investigations into organs of this sort, and their secretions and uses, were made simultaneously but independently by Delpino (6 and 7) in Italy, and Belt (2), in tropical America. While other observers have contributed many isolated facts to the knowledge of these organs in the fifteen years since the observations and conclusions of these naturalists were published, the task of following up and systematizing the distribution of protective nectar has de-

volved upon Delpino (8), whose evidently thorough studies are now in course of publication, the results already printed occupying over 150 quarto pages.

Broadly speaking, this class of extra-floral nectar-glands, by their secretion, attracts to the plants which bear them hordes of ants (rarely wasps), which constitute a temporary and changing body guard, disputing the presence of all other insects with the exception of their protégés the sugar-excreting aphides, coccids, etc., and resisting, often furiously and effectively, the onslaughts of ruminants and other large animals. That this is a true explanation of the reason for the existence of these structures, is generally admitted, today.*

The plants which possess such glands are phaenogams and ferns, chiefly of the tropics and subtropics; yet the number in our own and other temperate floras is rather surprisingly large.

The ants attracted by extra-nuptial nectar are mainly the omnipresent, omnivorous species. Protection is often afforded against various caterpillars and other leaf-eating larvae, as Ratzeburg (24) and others have observed; but the body-guard appears primarily destined to resist the depredations of other members of their own group,—the leaf-cutting ants,—which swarm in tropical and subtropical regions, and quickly defoliate plants not provided with this defence unless efficient service is rendered by colleters or alkaloids, which prevent the access of these insects to immature and tender parts, or render these distasteful to them. Delpino was at first inclined to explain the occurrence of protective nectar in regions where no leaf-cutting ants are found, solely with reference to herbivorous larvae. But it has been shown several times that such larvae are permitted in large numbers on plants provided with a body-guard of ants attracted by nectar. I have myself observed this in the case of *Gossypium*, which suffers notoriously from the attacks of *Aletia* and *Heliothis*, although it is unusually well supplied with extra-nuptial nectar that attracts numerous ants which to a certain but insufficient extent do attack the caterpillars of the moths named. The same thing is also to be seen on *Populus monilifera* in the west and south, where this tree is subject to very disastrous attacks from the larvae of a chrysomelid beetle, *Plagiodera scripta*, and a moth, *Acronycta populi*. Careful observations of the behavior of insects attracted by extra-nuptial glands, carried through a number of seasons, and on plants with differing surroundings, accompanied by correct identification of the insects are possible to local entomologists everywhere, and are much to be desired.

There seems little reason to doubt

* For a general negation of the prevalent notions concerning nectaries of all sorts, coupled with a good histological study of many of these organs, reference should be made to Bonnier's essay—Les Nectaires—in Annales des sci. nat., Bot., 1879, v. 8. also published separately at Paris,—which reverts to the theories of the last century.

It is also to be observed that Kerner von Marilaun, the learned Viennese biologist, quite recently describes the petiolar glands of *Populus* as organs of absorption Pflanzenleben, v.1. 215),— but without giving reasons for his belief nor an indication that another function had been previously ascribed to them.

that these protective adaptations are the result of natural selection, acting through the ages of co-existence of plants and their enemies. I have long felt a conviction that the occurrence of extra-nuptial nectar-glands on so many of our own plants which are not menaced by leaf-cutting ants (except in the extreme southwest), must date back to later geological periods, characterized by a warmer climate in northern latitudes, and by a much greater prevalence of ants of many kinds than is the case with us now* ; and that a corresponding prevalence of leaf-cutting or other noxious ants is demonstrable in these periods. Unfortunately, I have never been able to pursue the subject in this direction, but the immense collection of fossil ants in the possession of Mr. Scudder must furnish instructive data for testing this opinion, when its treasures shall have been sufficiently studied to show the affinities of the prevalent genera of those times in northern America. That structures corresponding in position to the foliar glands of existent species of *Populus* were found on tertiary plants, is shown by their occurrence on *P. glandulifera*, Heer (31, p. 290), but I do not now remember that they have been recognized elsewhere.

While, as has been shown, the secretion of food for protective ants is often rendered superfluous by the provision of other more direct deterrents, the two classes of protective adaptation sometimes occur conjointly. Lundström (16, p. 83) has shown that the leaves of *Populus* which do not possess nectar-glands are distinguished also by the thinness and flexibility of their compressed petioles, by which caterpillars, etc. are to some extent rendered uncertain in their footholds on these easily shaken leaves. Delpino and Schimper have also observed the protection secured to *Ricinus* by its smooth and very glaucous stems, though its leaves likewise bear extra-nuptial glands.

An aberrant function of the nectar-glands on the leaves of some pitcher plants is that of luring to their destruction, insects which are captured and digested or at least macerated by these carnivorous plants. From the large number of ants found in our *Sarracenia* leaves in a state of nature, this would seem to be true of species of this group ; for these ubiquitous insects are certainly led to the orifices of the pitchers by the sugary secretion on the exterior. In his latest paper (8, 227), Delpino holds this secretion to be protective, as in the cases already passed in review ; but the opinion which I have here and elsewhere (30, 328) expressed, is that of Riley (25, p. 25), Mellichamp (18, 119), Gray (10, 112), and others, some of them early writers on *Sarraceniaceae*. That ants are largely victimized by these plants does not, of course, signify that the structure of the latter is not such as to facilitate the capture of larger, flying insects, which are, in fact, often found entrapped, especially by the southern Sarracenias and the Californian *Darlingtonia*.

* On this point see a very instructive note by Mr. Belt in Nature, 1877, v. 16, 122.

Leave cannot be taken of the extra-nuptial nectar of phaenogams and ferns without reference to the sugary exudation which escapes on the emission of spermatia of *Uredineae*. As was shown by Ráthay (23), this is greedily devoured by ants and other honey-loving insects. But the service that these render, if any is rendered, is not clear, since it is not certain whether the spermatia are spores or male reproductive cells, though there is reason for considering them to be spores.* That ants play a considerable part in scattering these bodies is a necessary *a priori* conclusion; but it is not so evident how far the secretion of a sugary fluid is to be regarded as an adaptation to this end. It has recently been explained by Ludwig (15) in accordance with the Delpino-Belt theory.

2. Occasional Ant-domiciles on Plants.

Some part of a plant is not infrequently tenanted by ants which find there shelter or food to their liking, but so far as our own and other temperate floras are concerned, there appears to be no adaptation by which the plant is fitted to maintain or especially profit by this residence of ants. The heart-wood of some of our forest trees is often inhabited in this manner by the large black ant, *Formica pennsylvanica*. On several occasions I have also found an undetermined small brown ant nesting in the old hypanthia of *Calycanthus*, still adhering to the plant, in the botanic garden at St. Louis. No doubt any close observer of the ways of ants can add many instances of the same general character, in which, so far as the biology of the plant is concerned, the ants are merely accidental residents, though their pugnacity may lead them to resist the attacks of other creatures whose presence is distasteful to them.

It is also known that ants sometimes construct somewhat elaborate nests on plants. Some cases of this sort are noted by Westwood (34, 222) and Packard (21, 317), and I presume that a person more familiar than myself with entomological literature could cite other references on this subject. Several years ago I contributed to the Club the gist of observations on a colony of *Crematogaster* which had erected a nest over their wards, certain aphides, on a branch of *Andromeda*, where they apparently spent their entire time (Psyche, v. 3, 31). Similar nests had been observed before by others (Psyche, v. 3, 343; and the Minutes of the meetings held during 1883, 2). In the case observed by myself the ants appeared to be kept at their post by the aphides (which they may themselves have placed upon the plant), and the shelter was evidently constructed as much for these insects as for themselves. Where ants protect the enemies of a plant in this manner, they are clearly injurious to it in the first place, though they may at the same time keep off others of its enemies in endeavoring to guard their protégés. The good may even more than counterbalance the harm done, and Lundström has suggested that in

* See Plowright, managr. of British Uredineae and Ustilagineae, 1889, 11 *et seq.*

some cases aphides may be held as serving their host-plants in the capacity of wandering nectaries (16, 84). It is certain that they are sometimes a stronger source of attraction to ants than either nuptial or extra-nuptial glands.

3. Myrmecophilous Plants, proper.

Some of the earlier travellers, in describing their collections, make mention of the fact that cavities in the stems and stipules, or pockets on the leaves, of some tropical plants are tenanted by ants. This was recorded for *Cecropia* as early as 1648 by Marcgravius (17), and for *Acacia* in 1651, by Hernandez (12). Though scattering observations of more or less biological interest occur in the literature of the succeeding 225 years, it was not until the early part of the last decade that these plants received careful study. In 1872 Professor Caruel published a short paper (3) on species of *Hydnophytum* and *Myrmecodia*, two rubiaceous genera that had been known to harbor ants at least since the studies of Rumpf in 1750. The field notes and material for this paper were obtained from Beccari, who was led to believe that shortly after germination the bases of these plants are pierced by ants (subsequently identified as species of *Crematogaster* and *Iridomyrmex*) which tunnel the gall-like enlargement in various directions, making a permanent residence there. The plants were even thought to die while quite small if not pierced, though these attacks might have appeared necessarily injurious, to another observer. Later observations by Forbes (9) and especially by Treub (33) who has made good use of the unusual facilities afforded by the botanical garden at Buitenzorg in Java for cultivating tropical plants, seem to show that this puncturing of the stem is not so essential to the life of the plant as was supposed by Beccari; for in a series of cultures it was found that not only do young plants and seedlings develop when removed from all possibility of ant visits, but the excavations and perforations in their stems appear spontaneously. According to Treub, these elaborate structures, which in a state of nature appear to constantly serve as domiciles for ants, represent in reality a highly developed water-tissue, by which the plant is adapted to its epiphytic habit. The view that they are not primarily connected with the maintainance of a body-guard of ants, is accepted by Schumann (28, 419) in the last extensive study of myrmecophilous plants that I have seen, so that what have for years passed for ant-plants *par excellence*, seem likely to lose even a subordinate position in the growing category of plants of this class. Yet, as it seems to me, granting the full accuracy of Treub's observations, it by no means follows that the curious structure of *Myrmecodia* and related rubiaceous plants is not to be looked upon as an adaptation for providing a body-guard of ants with lodging; and it has been abundantly proved that they are ready to fight whenever they are disturbed in these residences.

At about the time when Beccari was making his first observations on these Malayan plants, Belt (2) was engaged in a similar study of the bull's-horn *Acacia* in tropical America, and here, as in the case of extra-nuptial nectar, the credit of having first recognized the protective signification of the structure, is shared by Belt and Delpino (6, 91). As a result of his studies and those of Francis Darwin (5) and Schimper (27), it seems to be definitely settled that in the spongy enlarged stipular thorns of several species of *Acacia*, certain ants find shelter, and are kept upon the plant by a sugary secretion similar to that which attracts wandering ants to so many other species of this and other genera, while in highly nutritious bodies at the tips of the leaflets is to be seen a further food-supply,—the three provisions securing their permanent residence.

Cecropia peltata and some other species of the genus are also known, thanks to Fritz Mueller (19), Francis Darwin (5), Schimper (27), and others, to produce upon their petioles food-bodies that are likewise eagerly gathered and eaten by ants, which inhabit the hollow stems of these species. Quite recently Schimper (27) has shown that in *C. adenopus* an unmistakable provision facilitating the entrance of the ants, exists in a thin soft spot observable on each internode of the hollow stem,—a fact which was indicated in 1876 for the Imbauba, by Fritz Mueller (4).

The number of species that may be classed as truly myrmecophilous, in that they afford lodging, sometimes accompanied by a provision of nectar or solid food, or both, calculated to maintain upon them a permanent army of ants, is already large. All are, so far as I know, phaenogams, but they are distributed through widely separated orders in this group. To Beccari, more than to any other single naturalist, is due the credit of having systematically undertaken their study in the field; and few biologists have published their observations so sumptuously as his appear in the volumes of his "Malesia." Unlike the plants with simple extranuptial nectar, these symbiotic plants often show a restriction in the species of ants which frequent them. And it is interesting to observe that closely related species sometimes inhabit myrmecophilous plants of widely separated regions.* Time will not permit me to enter into a more detailed discussion of the many cases of proved or probable symbiotic myrmecophilism, but enough has been said to show that on the one hand myrmecophilous plants join closely to those which provide food for a body-guard of ants which they do not furnish with a residence; while on the other hand they offer equally good transitions to those more or less constantly inhabited by ants which must seek their food from other sources than special secretions or derivatives of the plant. While both of these classes are represented in temperate climates, it is suggestive that the most highly specialized cases of myrmecophilism are not known to occur out-

* Cf. Schumann, *l. c.*, p. 416.

side the tropics, where, as the observations of Belt, Fritz Mueller, and others show, plants that do not possess some special and effective means of repulsion or defence are quickly stripped of their foliage, and where, from a persistance of this danger since the cooling of higher latitudes, natural selection has been kept in operation after it ceased to work great changes in this respect elsewhere. As might be expected, myrmecophilism in the more restricted sense may be replaced by other protective devices; and Schimper (27) has in fact shown that a tropical American species of *Cecropia* is enabled to dispense with the body-guard needed by its relatives, through having very glaucous stems, over which leaf-cutting ants cannot climb to its foliage.

In 1887, a rather remarkable paper (16) was published by Lundström, of Sweden, in which the hairy nerve-axils on the lower leaf-surface of oaks and other woody plants, the pits similarly situated on the coffee plant, etc., and a variety of other structures, were described under the name of domatia (diminutive of δῶμα, a house). The greater number of these are held for mite-domiciles (acaro-domatia), but it appears as if a fairly good series might be made from the simpler acaro-domatia to some of the more specialized pockets of leaves (myrmeco-domatia) inhabited by ants, that have especially been described by Schumann (28). If this is true, a plausible explanation of the one, when reached, may throw light upon the origin of the other. It may, therefore, be worth while to note that Lundström holds acaro-domatia for slightly specialized mostly hereditary structures that serve as a shelter for various mites, which benefit the plant by clearing its leaves of fungus spores which may fall upon them, and by contributing to their nutrition carbonic acid from their own respiration, as well as their excrement, exuviae, and, ultimately, their dead bodies. While this explanation appears far-fetched to most biologists, it is not unlike that applied by Beccari to the myrmecophilism of *Myrmecodia*, the ant-inhabitants of which are thought to contribute to its nutrition in a similar manner. Whatever the value of his hypothesis may be, it must be conceded that the Swedish botanist has brought together about them a large series of little known and unexplained structures, which can scarcely be looked upon as insignificant by the present school of utilitarian biologists.

In closing, attention should be called to the relations of ants to the seeds of plants. It is well known that in warm countries some ants carefully and systematically harvest the fruit of species which are to their taste, and it would appear that they also take some agricultural interest in the welfare of these plants. While this indicates a high grade of care for the food-producing species, the benefit to the plant is that which a cultivated crop receives from the self-interest of man in its preservation and propagation, without in any way approaching symbiosis.

The resemblance of some seeds or fruits to different kinds of insects or other arthropods has several times been commented on. Perhaps it is still an open question whether or not this is mimicry, but it has been so regarded by a number of naturalists, being held in some cases to secure dissemination by insectivorous birds, etc., and in others to render the detection of the seed by graminivorous birds, difficult. Suggestions are not wanting that in some of these resemblances, and some other seminal peculiarities, adaptations exist for securing dissemination through the agency of ants. Mr. Charles Robertson tells me that the arils of *Sanguinaria* seeds possess an attraction for ants, which drag the seeds off for considerable distances. I cannot say whether they finally eat these fleshy appendages. According to Lundström (16, 79), *Melampyrum* seeds resemble ant pupae in size and form, and, as he believes, in odor also, to such an extent that ants are deceived into caring for them as if they were their own pupae, until the mistake is discovered. Mimicry, such as he suggests, is a very difficult thing to prove to the satisfaction of unbiased biologists, but observations cited by him would seem to show that unusual attention is really paid to these seeds by ants which do not subsequently make use of them for food. The bracts of some species of this genus bear extranuptial nectar-glands, which Ráthay (22), who studied them carefully, could not explain by the protective theories of Delpino and Belt, or Kerner, though they are visited by ants. As the latter are thus attracted close to the fruit, Lundström suggests that the office of these nectar-glands may stand in close relation with the supposed mimicry observed in the seeds, — but this entire subject, while full of suggestion, is still in need of careful and comparative study.

References.

This list of papers mentioned in the preceding pages makes no claim to completeness. Many references to contributions as important as some of these might have been added, but the student who examines those that are cited here will find in them references to all that has been published elsewhere. A rather recent and very useful bibliography, although it is not complete, is that of Huth,—Myrmecophile und myrmecophobe Pflanzen, Berlin, 1887,—as no. 7 of his samnlung naturwissenschaftlichen Vorträge.

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