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Two Interesting Neotropical Myrmecophytes (*Cordia nodosa* and *C. alliodora*).

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At the Oxford meeting of the International Congress of Entomology in 1912 I presented a brief account of the bullthorn Acacias of tropical America and their relations to certain ants. I have since had several opportunities to investigate not only these, but also several other famous myrmecophytes belonging to the genera *Cecropia, Tachigalia, Cordia* and *Tococa,* and am endeavoring to summarize our knowledge of all the Neotropical ant-plants and their occupants. For presentation at this time I have selected two species of *Cordia,* namely, *C. nodosa* Lam., which I had occasion to study during the summer of 1920 at the Kartabo Biological Laboratory in British Guiana, and *C. alliodora,* of which I was able to examine thousands of specimens in the Panama Canal Zone during the early months of 1923 and the summer of 1924. These plants are chosen for special consideration, because recently the ant-inhabited cauline swellings of *C. alliodora* have been quite erroneously interpreted by a well-known Genevan botanist, Prof. R. Chodat and his collaborators Vischer and Carisso in their studies of the American species of Cordia (1920).

The botanists have divided the tropicopolitan Borraginaceous genus *Cordia,* which comprises some 230 species of trees and shrubs, into several sections, only two of which, the *Physocladae* and the *Gerascanthus* section, contain a small number of myrmecophytes. The great majority of the species are small trees of ordinary aspect which have nothing to do with ants. In the small section *Physocladae,* two closely related species, *C. nodosa* of Northern South America and *C. hispidissima* of Amazonas and Bolivia, are well-known from the studies of Schimper (1888), Mez (1890), Bailey (1924) and others. They are hairy shrubs or small trees, growing in damp places in the hylaea, or rain-forest. Just below each node, at which the verticillate, rather horizontal branches arise, the stem presents a fusiform, hollow enlargement, or swelling, which opens to the exterior by a preformed orifice. Such a swelling, which has the same fundamental structure in both *nodosa* and *hispidissima,* is known as a myrmecodomatium, because it is regularly inhabited by ants. According to Prof. I. W. Bailey, who collaborated with me in investigating *C. nodosa* in British Guiana, the cavity of the domatium is really formed by the invagination into the stem of one of the lateral shoots "and its formation may be likened to what happens when one

finger of a glove is retracted so that it ultimately projects inwards instead of outwards". This accounts for the fact that the cavity of the domatium is lined with hairy epidermis. No one who has studied the domatia of the *Physocladae* in living plants has ever doubted that they are preformed structures and therefore neither insect nor fungus galls.

The domatia of *nodosa* and *hispidissima* are inhabited by some 21 different species, subspecies or varieties of ants, 11 of which belong to the genus *Azteca*. All of these insects, with a single exception, are small forms which offer but feeble resistance to handling or interfering with the plant. The single exception is *Neoponera unidentata* Mayr., which stings severely, hut makes only small colonies in a few of the domatia and is often absent. Indeed, it nests more frequently in the dead branches of other trees or bushes. The most interesting occupant of the *nodosa* and *hispidissima* domatia is *Allomerus 8-articulatus* Mayr, of which I have been able to recognize four different varieties in different parts of South America. The British Guiana form, var. *demerarae* var. nov. is well-known to the native Indians, who call it the "kurabelli" (Hohenkirk, 1918). Its colonies are extremely populous, comprising thousands of workers and many mother queens. Each colony normally occupies all or most of the domatia on a *nodosa* bush or tree. All the cavities are connected with one another and with the forest floor by a peculiar system of galleries or arcades, constructed by the ants on the surface of the plant and measuring about 5—10 mm in diameter. They consist of minute particles of black, agglutinated earth built up around and supported by the long red hairs that cover the surface of the trunk and branches. A single arcade starts at the ground and ascends the trunk to the first node where it sends a branch along the surface of each limb of the verticel. The branching is repeated at each succeeding node till each domatium is furnished with a gallery that runs up its side and terminates at its orifice. The minute, pale yellow, small-eyed workers are thus enabled to pass under a continuous carton-like roof and between the stiff hairs which support it like so many pillars, from their nests in the domatia to the ground, where they forage among the dead leaves. Coccids *(Pseudococcus brevipes)* are found in some of the domatia, but they are not sufficiently numerous to provide more than an insignificant portion of the food required by so large an ant-population. This consideration and the elaborate construction of the arcades show that while the *Cordia* furnishes most admirable living-quarters for the ants, it is by no means an adequate source of food.

During the rainy season (July to September 1920) I found the cauline swellings full of the kurabelli brood in all stages, together with many males and females. The sexual forms are much larger and darker colored than the workers. The rather peculiar larvae will be described by Dr. G. C. Wheeler in a forthcoming paper. As soon as the domatia on the youngest branches become large enough, deälated females take possession of them and begin, apparently at once, to lay eggs. And though each incipient swelling usually contains only a single young deälated female, I have on several occasions found two, three or even four such individuals, all caring for their eggs or young larvae in common in the same cavity. Unlike most ants, therefore, *Allomerus* is frequently

pleometrotic even during the incipient stages of colony formation. After they are reared, the broods of these young females undoubtedly become a part of the single large polycladic colony which possesses the whole plant.

It cannot be maintained that the kurabelli act as an efficient protective body-guard for the *Cordia,* at least so far as man and the larger animals are concerned. When one handles the plant for some time, the workers do indeed swarm over one's clothes and body and keep on stinging for some time, but their stings are so minute that they produce only a rather unpleasant itching and that only on parts with very thin epidermis. While it is more probable that the kurabelli may be more efficient in keeping the plant free from certain insects, it should be noted that other *Formicidae* not infrequently occupy some of the domatia, though most of them may be tenanted by *Allomerus,* and both Professor Bailey and I sometimes found the foliage of such plants considerably damaged by leaf-cutting ants *(Atta cephalotes).* I have also noticed leaves that had been extensively gnawed by caterpillars, and the foliage of one plant tenanted by *Allomerus* was covered with Cecidomyid galls. The only other insects found associated with *C. nodosa* were termites, which on one occasion were seen to have a gallery extending up the trunk from the ground and terminating in a cauline swelling which they were occupying.

According to Chodat and Vischer (1920) the *Gerascanthus* section of *Cordia* comprises some 17 species. Unlike the *Physocladae,* they are tall shrubs or trees, frequently attaining a height of 20 to 40 feet, with smooth gray bark and coriaceous, opaque leaves, covered with dense stellate hairs beneath and sparser hairs of the same type above. The branching, except in young specimens, is much more obscurely verticillate, and though ant-inhabited cauline swellings occur at the nodes in some of the species, they are much simpler, being merely conical, pyriform or turbinate dilatations of the stem, with large medullary cavity and without a preformed orifice. The flowers are more showy and usually aggregated in broad, dense panicles or corymbs. As a rule, the plants grow on higher ground, in the campos or more open woods and thickets, and therefore in more xerothermal situations than the *Physocladae.*

Chodat and Vischer enumerate 9 of the species of the *Gerascanthus* section as possessing cauline swellings and therefore as being myrmecophilous, but these authors confuse the whole matter by failing to distinguish carefully between galls and preformed domatia. In their opinion, which is based very largely on examination of herbarium material, all the stem swellings are insect galls which are later inhabited by the ants. That this conclusion is eroneous appears from an examination of two species which they fail to distinguish, namely *C. gerascanthus* L. and *C. alliodora* Ruiz and Pavon. The former, which is a large-flowered species of the Greater Antilles, may occasionally have galls, but never has domatia, whereas the small-flowered *C. alliodora,* which ranges from Mexico to Bolivia and Brazil, always has domatia and may occasionally bear galls of the type described by the Genevan botanists. Probably the plant of which I observed all stages in Panama is really a variety of the true *C. alliodora* of Peru. It has been passing as *C. gerascanthus* Jacquinius (nec L.) in the literature, and Chodat

calls it forma *micrantha* of that species. According to Dr. *I. M. Johnston* of the Gray Herbarium *(in litt.)*, however, the Mexican and Central American form should be regarded as a geographical variety (to be named by him in a later publication) of *C. alliodora*. That *C. gerascanthus* and *C. alliodora* must be specifically distinct is clear from the constant presence of domatia in the latter and their complete absence in the former *).

The association of ants with *C. alliodora* has been noticed by several observers. Ruiz and Pavon (1799) refer to it, though they neither figure nor mention the domatia. These structures and their occupants were, however, observed by Spruce (1869) in Brazil, and Beccari (1884) figures a characteristic domatium from a Mexican specimen of the tree. More than 20 years ago Mr. C. H. T. Townsend sent me from Mexico not only specimens of the domatia, ants and Coccids, but also notes on their interrelations. More recently Ule (1907) has made similar observations in Peru and Mann in Bolivia. Menozzi (1927) has also published an account of the domatia, ants and Coccids from material taken by H. Schmitt in Costa Rica. In the accounts of Spruce, Beccari, Ule and Menozzi the tree is cited as *C. gerascanthus* Jacquinius.

I found *C. alliodora* to be a common tree on the Pacific side of the Panama Canal Zone, less common on the Atlantic side near Colon. There are many specimens of it on Barro Colorado Island, in Gatun Lake. From Frijoles to Ancon it is often a conspicuous component of the second growth jungle and in the clearings, but usually avoids moist spots and shows a preference for the slopes of hills. It comes into flower during the last days of February and continues to bloom profusely till about the last of March. During this portion of the dry season the large compact racemes of small white blossoms make the trees conspicuous objects in the landscape. Seedlings and young trees of all sizes can be found singly or in colonies, especially about clearings and along roadsides, so that the plant can be readily studied in all stages. The largest specimens attain a height of 30 or 40 feet. Flowers are not produced till the tree is about 10 or 15 feet high. While young (below 4 to 6 feet) it is usually very symmetrical, with the branches coming off in regular whorls at intervals along the straight, slender trunk, so that in this stage it somewhat resembles adult specimens of *C. nodosa*. Later the branches vary much more in length and direction and are less horizontal. Eventually the crown of foliage may be either irregularly pyramidal or, especially when growing in the open, more diffuse and spreading. The trunk and branches are slender and graceful, with rather smooth, gray bark. The ovate, coriaceous leaves are two to four inches long and grayish green, with rough margins. There is considerable variation, however, in the texture and surface of the leaves. The flowers have a strong odor, somewhat like that of decayed urine. They soon turn brown and persist for some time, often till the middle of April, but later fall off and the same is true of the stems of the inflorescence, though its base, which has a well-

*) The detailed discussion of this taxonomic tangle is reserved for my final paper.

developed swelling, or domatium, may remain behind as a dead, dry structure for at least a year.

An examination of fully developed trees shows that there is almost invariably an ant-inhabited d o m a t i u m at each node and that these swellings grow larger successively the nearer they are to the bases of the branches, but the stoutest branches and the trunk exhibit little or no enlargement in the corresponding regions. Here the d o m a t i a persist, nevertheless, but are concealed by a normal and very considerable growth in the thickness of the wood.

It is a singular fact that the adult *alliodora* trees lose their leaves during the rainy season, when all the other trees of the Panamanian jungle are in full foliage. During July and August the bare trunks and branches stand out as if dead among the dense green foliage of the other trees and the very regular arrangement of the d o m a t i a at the insertions of the branches are visible from afar. These trees could thus be located with the field-glasses among the tree-tops around the laboratories at Ancon and on Barro Colorado Island.

My attention, like that of C h o d a t and his collaborators, was at first directed to the inflorescences, by finding distinct elongate thickenings of some of the small flower-stems, and I, too, at first took these thickenings to be the initial stages in the formation of the ant-inhabited cauline swellings. In the former I also occasionally found minute, maggot-like larvae, but did not succeed in rearing the adult insects. They were Hymenopterous and very probably the larvae of the Eurytomid observed by the Genevan botanists, or of some allied species. But most of the enlargements, which are only 2 or 3 mm in diameter, contain no traces of eggs or larvae and are filled with a uniform and undisturbed mass of brown pith. I am certain, therefore, that they are not galls, but merely occasional preformed thickenings of the flower stems, in which the Eurytomids lay their eggs. In other words, these thickenings are strictly limited structures which precede the infection and are not produced by it. The Eurytomid (?) larvae simply feed on the pith which happens to be more abundant in the thickenings than in other portions of the flower stems. That these thickenings do not become the true nodal, or cauline swellings inhabited by the ants, is proved by the fact that they wither and drop off after flowering and cannot therefore produce persistent, leaf-bearing branches. True woody galls are, however, sometimes produced on the twigs of the tree by some unidentified insect, but these galls are very different in shape and texture from the d o m a t i a.

In order to ascertain the origin of the cauline swellings it is necessary to investigate the seedlings and young Cordias and the suckers that often grow up from the roots of larger trees that have been felled. These juvenile stages present a very different picture from that described by C h o d a t and V i s c h e r. The plants are green throughout and actively growing and, as I have stated, very symmetrical in the arangement and length of their few branches. The stem immediately below each of the nodes is regularly swollen and turbinate and forms a rather thin-walled, green capsule, closed on all sides and varying according to its age from 5 to 15 mm in diameter. The delicate remnants of the pith form an even layer over the wall of its large cavity, w h i c h c o n t a i n s n o

traces of any insect parasite. Nor do the great majority of juvenile trees or suckers harbor any ants till they reach a height of about three to five feet. The swellings are so perfectly regular and symmetrical in their arrangement, so comparable in position with those of the Cordias of the *Physocladae* group and so constantly present, except in the youngest seedlings less than a foot in height and with only the first whorl of leaves, that no botanist, and certainly no entomologists, can possibly regard them as galls. Very occasionally there may be no domatium at a node where it might be expected to appear, but this sometimes happens also in the *Physocladae*. Such infrequent and sporadic failures or inhibitions of development do not invalidate the general conclusion that the domatia of *C. alliodora* are quite as certainly preformed structures as those of *C. nodosa*.

Except in the domatia at the very base of the inflorescence, which, as previously stated, may persist and dry up when the latter falls off, there is a gradual growth in the thickness of the woody walls and in the size of the enclosed cavity. The ants perforate and enter the domatia very soon after their walls begin to lignify. I have not been able to follow the details of the process, although I have frequently found single young dealated females of various species and notably of *Azteca longiceps* Emery either alone or with their first brood of larvae in the swellings. The perforation or perforations, for there may be several, are always made in the thinner portion of the wall below the node, but there is no regularity in their position. In many cases the opening made by the entering queen closes through growth of the plant tissues and has to be reopened by the first brood of workers. The continued growth of the domatium after its occupation must be due to the constant irritation produced either by the ants or by the numerous Coccids which enter it, and attach themselves to the walls of the cavity and sink their delicate mouthparts into the plant tissues. That the Coccids may be the more potent irritants seems to be indicated by the conditions in the various Aphid and Psyllid galls of north temperate regions and the Coccid galls of Australia. In the case of *C. alliodora*, the Coccids may be responsible not only for the irregular shapes assumed by many of the domatia in their later stages, but also for the unequal vigor and growth of the older trees.

That the growth of the domatia does not continue indefinitely is shown in longitudinal sections of the nodal regions of the trunk and larger branches of old trees. The cavity soon ceases to enlarge, but the layers of xylem in its walls increase so enormously that the external swelling is obliterated. Concomitantly with this growth in the xylem the perforations, or entrances to the cavity, develop as long tubular galleries which traverse the whole layer of wood, radiate from the central cavity and open on the surface of the bark at points several inches apart. Although even at this stage the cavities may still be inhabited by ants, the Coccids have all disappeared, probably because their food-supply has been completely shut off by the development of the very thick layer of wood between the cavity and the cambium.

The regular development of the swellings, or domatia in *C. alliodora* and other Cordias with such preformed structures, thus presents a

very interesting problem to the plant-anatomist interested in phylogeny. Attention may be called in this connection to similar structures in at least one other plant belonging to a very different genus, all the other species of which have stems of the normal unswollen type. This is the Polygonaceous genus *Eriogonum*, which comprises about 100 species in the United States west of the Mississippi. The single species, *E. inflatum* Torr., has hollow, fusiform swellings at the upper ends of the internodes of the stems and branches. I have observed this plant at Palm Springs, Cala, in the Mojave Desert, at the foot of the San Jacinto Mts. It is one of the few perennial species of the genus, according to Tidestrom (1925), who cites it as belonging to the "desert areas and hillsides of the Covillea and Artemisia belts" in South-western Utah, Colorado, Nevada, Arizona and California. The swellings are not inhabited by ants, probably because all the *Formicidae* in its desert environment are earth-nesting forms. But there is no doubt in my mind, that if the plant were to invade the tropics, certain species of stem-inhabiting ants would at once take up their dwelling in its hollow swellings. Under these circumstances *E. inflatum* would become a regular myrmecophyte like *C. alliodora.*

During my two seasons in Panama I took pains to collect not only all the ants, but also all the other organisms more or less closely associated with *C. alliodora;* in other words, to make an inventory of the biocoenosis of which the plant is the center or focus. Most of these organisms have now been identified with the aid of a number of specialists, and I am able, in advance of a more detailed account, to make a few summary remarks on the more important *C. alliodora* tenants. Omitting the bacteria, fungi and nematodes, my list comprises 211 different Arthropods, 58 of which are ants. Of this number 48 live in the domatia, two *(Azteca xysticola* and *instabilis)* in the trunk and 8 live in the ground, but visit the foliage for the purpose of attending Coccids, Aphids and Membracids, or possibly in one case *(Atta cephalotes)* for the purpose of cutting the leaves. The great majority of the domatia-tenants occur also in dead twigs of a great variety of trees and shrubs. Probably only four of the species collected, namely *Azteca longiceps* Emery and its subspecies *balboae, cordincola* and *patruelis, A. pittieri* Forel and its var. *emarginatisquamis, Pseudomyrma sericea* Mayr and its var. *cordiae* and *Ps. alliodorae* sp. nov. are to be regarded as obligate tenants of the plant. Of these *A. longiceps* is the most abundant and occurs in about 85% of the domatia on nearly all the trees.

In order to examine the ants and their brood Mr. James Zetek and I adopted a method which we also employed successfully, with obvious modifications, in dealing with other myrmecophytes *(Triplaris, Acacia, Cecropia, Clerodendron, Tillandsia).* We either cut down the tree, or when this was impracticable, lopped off large branches. Then with a pair of strong pruning scissors we cut out the domatia and carried them in cloth bags to the laboratory, where they were placed in a large jar. Some chloroform was poured on the bags and the jar covered till the insects were asphyxiated. The domatia could then be cut open and their contents examined at leisure. We found that few of the ants left their nests to die in the bags and that the domatia, even when

they were inhabited by different species, contained all or nearly all of their original inhabitants.

A number of the *C. alliodora* ants, especially those of the genera *Crematogaster, Leptothorax, Tapinoma* and *Camponotus*, are very sporadic, occuring in only a few domatia on a tree or branch. *A. longiceps* is certainly the common and dominant tenant in nearly all the localities in which I collected. It usually occupies most or all of the domatia, especially those at the base of the branches, while the sporadic species inhabit by preference the terminal and especially the dead and dried swellings that bore the inflorescences of the previous season. Not only *A. longiceps* and *pittieri*, but also several of the other species keep living Coccids in their nest cavities. Unlike the large aggressive Azteca which either construct large pendent carton nests on various trees or form populous colonies in their trunks, *A. longiceps* is a small, timid and rather lethargic ant. This is indicated both by its toleration of other ant-tenants and other insects on the same tree and by the fact that I have sometimes cut up Cordias for hours without being bitten more than half a dozen times by the larger workers. The *A. longiceps* inhabitants of all the domatia on a tree constitute a single polycladic colony, which keeps growing and spreading by successive occupation of new swellings as fast as they attain the proper size on the growing twigs. During March and April the domatia contain much brood in all stages together with many males and winged females. The domatial cavities are lined with a thin layer of brownish or blackish substance and contain a black or dark brown mass of carton, made up of a net-work of trabeculae like those constructed by some other species of Azteca that nest in plant cavities. This structure was seen by Beccari, Chodat and Vischer and Menozzi, and consists of very finely and uniformly triturated and agglutinated particles of wood and pith. I have failed to detect in it any pollen-grains, leaf-fragments or stellate hairs, such as were found by Chodat and Vischer, but would not deny that these substances may sometimes be employed by the ants in the confection of the mass. It is obviously a kind of scaffolding which subdivides the original cavity into smaller compartments and galleries in which the brood can be spread out and more easily cared for. The mass can be readily removed in its entirety, because it is rather feebly attached to the walls of the cavity. Chodat's and Vischer's contention that the ants "dévorent une partie des feuilles et récoltent le pollen" is highly improbable. I have never seen the ants visiting the flowers and they certainly do not devour the leaves. But even if this were true, and if the carton were made of leaf material as these authors maintain, the combined mass of it in all the domatia on a tree would be too small to represent any serious damage to the plant.

In the spaces surrounding the mass of carton and sometimes almost covering the walls of the cavity are the numerous Coccids, among which at least three kinds of species may be readily distinguished. The majority are flat lecanoid forms of a pinkish color and varying considerably in size. Among them may be found small, snow-white Pseudococci, either singly or in clusters and several large, subglobular, shining black or red forms belonging to the genus *Cyclolecanium*. All the Coccids collected on *C. alliodora* by Mr. Zetek and myself were carefully studied by Dr.

Harold Morrison (1929), who recognized 14 species among them. Five (3 species of *Saissetia,* one of *Coccus* and one of *Aspidiotus)* live on the twigs and leaves, but nine (1 *Akermes,* 3 *Cryptostigma,* 1 *Cyclolecanium* and 4 *Pseudococcus)* live in the domatia with the ants. These Coccids suggest interesting problems and reflections. They are present in such numbers that they must provide their hosts with a copious supply of honey-dew. That the large *Cyclolecanium* breed in the domatia is indicated by the fact that they are often found to be filled with eggs and, owing to their size, are quite unable to escape to the surface of the plant through the tenuous openings in the walls of the domatia. But whether the Coccid colonies are originally established by young individuals that crawl into the domatia from the surface of the plant or are carried in by the ants, cannot be decided without further observation. Judging from what is known of some other ants *(Lasius* species, *Iridomyrmex humilis,* etc.), the latter alternative would seem to be the more probable.

There is also in the cavity of each domatium occupied by *A. longiceps* another singular object, which has been overlooked by previous observers. The funnel-shaped lower end of the cavity is filled with a small conical plug of moist substance, which can be readily removed as a coherent mass and on examination proves to have a very complex structure, consisting of the ejected infrabuccal pellets of the ants, moulds, innumerable bacteria and small nematode worms. Its more liquid portion is probably the faeces of the ants and such honey-dew from the Coccids as happens to drain down the walls of the cavity and has not been intercepted and imbibed at its source. We may therefore regard the lowermost funnel-shaped end of the domatial cavity as a veritable public latrine or cesspool. The nematodes have been studied by Dr. Cobb, who informs me that they are unusual from the taxonomic point of view. The moulds and bacteria which flourish in the faecal material of the latrines may afford interesting study for some future student.

Among the other ants of the *C. alliodora* domatia two sluggish and timid species of *Cryptocerus* of the subgenus *Cyathocephalus,* namely *C. pallens* Klug and *C. setulifer* Emery, are of unusual interest. because their females and soldiers have the top of the head developed as a large, broadly elliptical, dish-shaped structure with which they can close the entrance to the domatial cavity. The behavior of these ants is therefore very much like that of the species of *Camponotus* of the subgenus *Colobopsis.* In the latter, however, the front instead of the top of the head exhibits this singular phragmotic modification. Not only is the cephalic dish exquisitely fitted to fill the elliptical nest entrance, but as a result of its long exposure to the elements, the concavity, especially in *C. setulifer,* becomes filled with a compact layer of dust and greenish brown particles that so closely resemble the lichens and algae growing on the bark of the domatium that it is difficult to detect the position of the opening when the soldier or queen is on guard.

If we consider only the Arthropod participants in the *C. alliodora* biocoenose, or community, we have in the following table the numbers of different forms in each of the larger groups:

Arthropoda of the Cordia alliodora Biocoenose.

Hymenoptera (including Formicidae)	69
Lepidoptera	6
Diptera	14
Coleoptera	39
Orthoptera	13
Thysanoptera	2
Neuroptera	2
Heteroptera	10
Homoptera (including Coccidae)	35
Myriopoda	2
Arachnida	18
Isopoda	1
Total	211

Of course, the composition of the biocoenose of a plant so widely distributed as *C. alliodora* must differ considerably in different parts of its range, and, no doubt, the foregoing table, which, apart from the ants, is based almost entirely on collections made in a very limited area, represents a mere fragment of the total Arthropod fauna infesting the tree. It is sufficient, nevertheless, to dispel any notion that the plant must derive some peculiar advantage in the way of protection from the ants that constantly occupy its domatia after it has grown to a height of three or four feet. Before that time and when protection would seem to be most needed it can receive none, as we have seen, because it is not yet inhabited by colonies of ants but only by the solitary queens imprisoned in the domatia. In addition to some insects that visit the flowers, a number of spiders that lurk or spin their webs among the branches and a few beetles that bore in the trunk, the table also includes quite a series of forms which cause serious injury to the most sensitive part of the plant, the foliage. Some of these leaf-eating species may be very briefly considered.

At Ancon no less than six different moth-caterpillars were found by Mr. Zetek and myself devouring the leaves of the seedling and young Cordias, and at least one, the Pyralid *Conchylodes salamisalis* Druce, gnaws great holes in the leaves and with the fragments constructs a very regular, ellipsoidal cocoon. Before pupation it spins a silken tent at the base of the leaf as a temporary retreat. Among the Chrysomelid beetles, the Cassidine *Psalidonota leprosa* Boheм., which in life looks like a large drop of molten gold, passes its entire larval and pupal life on the foliage. Indeed, it is so abundant that *C. alliodora* must be its true host plant. Numerous grasshoppers, especially *Osmilia flavolimbata* De Geer and *Coscineuta coxalis* Serv., both as nymphs and adults, devour the foliage. A small Thrips is abundant on the leaves, which are also seriously injured by an undetermined red spider and all stages of a small Tingitid, *Monanthidia monotropidia* Stål. Another Heteropteron, the Pentatomid *Edessa collaris* Dall., also occurs in numbers and in all stages on the foliage of young Cordias. If we add to these various forms at least 20 different Homoptera, including Membracids, Cicadellids, Jassids, Aphids,

Psyllids and Aleurodids and the 14 species of Coccids, cultivated by the very ants that might be expected to protect the plant, it becomes clear that *C. alliodora* can enjoy no more immunity from insect enemies than any other tropical tree. It seemed to me to be even more heavily infested than many other members of the Panamanian hylaea, but this may have been due to my greater interest in its fauna.

The studies which I hope to publish on the other neotropical ant-plants of the genera *Triplaris, Tachigalia, Cecropia, Acacia, Tococa,* etc., all show conditions very much like those of *C. alliodora.* Each of these plants is the center of a considerable and heterogeneous biocoenose, and in this respect is quite like any non-myrmecophilous plant. I therefore conclude that the usual plant myrmecophile theories which imply survival and the development of domatia, etc., through natural selection are simply "bunk", and agree with Dr. von Ihering when he contends that the myrmecophytes have no more need of their ants than dogs have of their fleas. In the tropics ants are so very abundant and ubiquitous that they will occupy any available vegetable cavities to which they can gain access. Of course, certain species or genera of ants have become hereditarily attached to certain species or genera of trees. When the trees develop nectaries or food bodies in addition to domatia, as in *Cecropia* and the bullthorn Acacias, the relationship established between the trees and the ants is that of host and parasite. In most other cases a similar relationship results from the intercalation of Coccids, which behave like nectaries so far as the ants are concerned. The extraordinary problems of the phylogenetic origin and physiological significance of the domatia, food-bodies and nectaries, however, are purely botanical, and up to the present time we have not made the slightest approach towards their solution.

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