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Hunt Institute was dedicated in 1961 as the Rachel McMasters Miller Hunt Botanical Library, an international center for bibliographical research and service in the interests of botany and horticulture, as well as a center for the study of all aspects of the history of the plant sciences. By 1971 the Library's activities had so diversified that the name was changed to Hunt Institute for Botanical Documentation. Growth in collections and research projects led to the establishment of four programmatic departments: Archives, Art, Bibliography and the Library.

Ant-Gardens and Ant-Hotels.

By Rudolf Beer, B.Sc., F.L.S.

It is difficult for us who live so far away, and under such different circumstances, to realise the enormous influence that the leaf-cutting ants exert upon the vegetation of the Western tropics. Horticulturists from South America tell how impossible it is to introduce many fruit trees and vegetables into those countries solely because they are destroyed by the leaf-cutting ants as soon as they are planted.

To anyone who has had the opportunity of watching the restless energy which the countless hordes of these tiny animals display, it is a matter of wonder that a leaf is left upon any plant. It is partly owing to the wonderful exuberance of a tropical forest that the trees are not all stripped entirely bare, but it is more often due to various protective adaptations that the plants escape destruction. To these adaptations we will return in a later section of this paper. One of the most vivid descriptions of the leaf-cutting ant which we possess is to be found in that classic of natural history—Thomas Belt's "The Naturalist in Nicaragua" (1874). In this work Belt describes how the tracks of the leaf-cutting ant spread in every direction through the forest. Over these paths two great armies of ants constantly move; one hastening away from the nest into the forest, the other returning to its home laden with a piece of leaf about the size of a sixpence. If one of the ants hurrying from the nest be followed it will be seen to ascend some distant tree or bush, and, with its scissor-like mandibles, to cut a slice from a leaf, with which it hurries away. So numerous and so active are these ants that in a very short time nothing is left on the tree but the leaf-stalks and some of the harder ribs of the leaf. The tracks of the ants often range for more than half a mile from the nest. Besides his splendid observations upon the work and habits of these ants outside the nest, Belt has guessed with wonderful acumen at their behaviour within their home and the use they make of the leaves they so laboriously cut and carry to their abode. So extraordinary and so improbable, however, did this guess seem that very little credence was given to it until the whole subject was re-opened by the exhaustive labours of Alfred Möller* in Brazil.

Möller was stationed at Blumenau, and here he found the most common species of leaf-cutting ant to be *Atta discigera* (Mayr). *Atta hystrix* (Latr.) is almost equally abundant, whilst *Atta coronata* (Fabr) is much rarer. Another species of *Atta* which Möller provisionally calls *Atta IV.* is occasionally met with in the woods round Blumenau, but it forms only small colonies.

The paths which these ants make (speaking here of *A. discigera* in particular) are beautifully smooth and form little hollowed-out channels, over half an inch across, which extend in all directions from the nest. One path Möller traced for upwards of 26 yards across a meadow. Most of this path was completely hidden and protected by the grass, but wherever it was left exposed the ants had roofed it over with an earthen cover. Besides the ants which were carrying leaf-fragments and those which were hurrying away to fetch fresh loads, others were seen moving, in an apparently aimless fashion, along this path. When, however, any spot on the road was broken down or an obstacle placed on the path, whilst the leaf-carrying ants tried to find a way round it, the aimlessly-moving ants suddenly showed a purpose in their movements and hastened to the obstructed spot, where they formed a regular breakdown gang, building up the broken way or removing the obstacle in a very short time. Möller and a friend who was with him watched the journey of one particular ant which was carrying a load that weighed about double its own body weight. They found that it travelled over the 26 yards in about 1 hour 10 minutes.

The actual cutting out of the leaf-fragment was repeatedly watched by Möller with the aid of a magnifying lens. The ant sits on the piece of leaf that it is cutting away and uses its mandibles as scissors; all the time that this is going on it turns itself slowly about on its hind legs. As it sits upon the slice of leaf which is being cut out it looks as though the ant must fall to the ground together with its burden, but just at the last moment it is seen that the little animal has stretched out one of its fore feet with which it grasps the attached leaf and that, although at the moment that the fragment of leaf is detached the ant appears in a perilously uncertain position, it almost immediately rights itself and hoists up its load into a convenient position and then it hastens upon the return journey to its home.

The weight of the load carried by the ant was several times ascertained. As a rule it is from one and a half to two times the weight of the ant, but in other cases it is much heavier. In some extreme instances it was found that an ant was carrying a burden nine times its own weight!

The nests of *Atta discigera* and *A. hystrix* are rarely built in the open. In such cases they are seen to be bluntly pyramidal structures the surface of which is made up of pieces of dried leaf and stick. In nearly all cases, however, the nests are formed in little natural hollows which may be enlarged to a suitable size by the ant. One large nest had been built under the stone steps of the house in which Möller was staying.

Inside every nest, wherever and however built, there is always a loose, soft, grey, flocculent, porous mass which is channelled and hollowed like a sponge. This mass was called "ant food" by Thomas Belt, and the "Pilzgarten" by Möller. I will call it the *ant-garden* in the present paper.

This ant garden contains the eggs, larvæ, and pupæ of the ants in its pores and passages; it is always free from the walls of the nest, but is never found uncovered. *Atta coronata* usually builds its nests underground, and not infrequently it bores for more than a yard below the surface before it constructs its "garden."

The nests of *Atta IV.* are similar to those of *A. discigera*, but on a smaller scale. If a fragment of the ant-garden be broken off and examined under a lens it will be seen to be composed of numberless little soft pellets, each about $\frac{1}{20}$th of an inch in diameter, which build up the garden like bricks do a house. These pellets, when they are quite fresh, are dark green, older ones are almost black, whilst very old ones are yellow-brown in colour. They are interwoven with the threads of a fungus, and it is these threads which take the place of mortar and bind the pellets together into the mass of the ant-garden. Spread over the entire surface of the "garden" are an enormous number of little, round, white bodies varying from between $\frac{1}{50}$th and $\frac{1}{100}$th of an inch in diameter. Möller has called these the *Kohlrabi-heaps*. These "Kohlrabi-heaps" are part and parcel of the fungus which interweaves the pellets of the garden and under the microscope are seen to be little round swellings upon the superficial threads of the fungus.

As was pointed out at the beginning of this paper, it

* His work is recounted in "Die Pilzgärten einiger Sud amerikanischer Ameisen." Gustav Fischer, 1863.

has been well known for many years that these ants cut and carry fragments of leaves to their nests. The number of leaf-fragments which thus reach the nest is very large. Möller observed 217 loaded ants to pass one point on a path leading to the nest in a quarter of an hour, and in Nicaragua the number of ants which move along the tracks is far greater. In spite of this no leaf-fragments accumulate in the nest itself, and their fate has been the subject of much wonder and surmise to many naturalists. Some have believed that the ants eat the pieces of leaf, others imagined that the nest was built of these fragments, and, finally, Thomas Belt hazarded a guess of the most sensational character as to the use which was made of the pieces of leaf.

He believed that the leaf-cutting ants were gardeners and that they actually prepared beds with the leaf-fragments that they brought to the nest, and that upon these they grew a fungus for their food. "I believe," he writes, "that they are, in reality, mushroom growers and eaters."

Belt's supposition was of so remarkable a character and he was able to bring forward so few facts to support it that, although it attracted a great deal of attention, it found but few adherents.

Möller, armed with the resources of a splendidly-equipped laboratory, attacked the problem with an ingenuity of mind and an untiring enthusiasm which must win for him our highest admiration.

That the ant-garden is greatly valued by the ants is shown by the scrupulous care with which they gather up every fragment of a "garden" that has been removed from a nest and scattered on the ground. If a nest is several times disturbed its inhabitants will desert it and make their home elsewhere. When this is done, however, they carry with them not only their eggs and larvæ, but every morsel of the "garden." Möller next examined the ant-garden microscopically, and he was able to ascertain that the pellets of which it is built consist of torn shreds of leaf. Stomata, epidermal cells, and chlorophyll grains could all be seen in these pellets. There was strong reason to believe, therefore, that some, if not all, the pieces of leaves which are carried to the nest are shredded out and worked up into these tiny little soft building-stones of the garden.

The next step which Möller took was the attempt to keep the ants in captivity under such conditions that he could constantly watch their operations.

After many failures he at last succeeded in this attempt.

In a covered glass basin he placed a few workers of *Atta discigera* or *A. hystrix*, and, after crumbling up a piece of "garden" to tiny pieces he scattered these over the bottom of the basin. The ants at once set to work at the pieces of garden, and within 12 hours they had reconstructed a new garden. All bits of dirt or other foreign matter were carefully separated and set on one side. Continuing his observations on the following days, Möller noticed that the older pellets, upon which the fungus no longer grew, were removed from the garden and added to the heap (or, rather, layer) of refuse. As this goes on the nest becomes smaller and smaller until at last nothing is left of it. The ants then run aimlessly about, and after eight to 14 days they are all dead. From this it is seen that the life of the ant is bound up with the existence of the "garden."

In another experiment a little moist sand was placed in the glass vessel, a few leaves of a plant the ants usually "cut," and a certain number of ants. The ants burrowed into the sand, but never touched the leaves. After some days' starvation a small fragment of "garden" was introduced into the basin. An ant moved to it, and, after examining it, hastened under the sand to return almost at once accompanied by the other ants. These all hurried to the "garden," and, watching them under a magnifying glass, Möller could see that they greedily tore off and devoured the Kohlrabi-heaps of the fungus. Again Möller starved ants for several days and then presented them with the Kohlrabi-heaps of the fungus upon the end of a needle. These they at once seized and ate.

Finally Möller kept a number of ants in a glass basin, together with the fragments of a "garden" and several leaves from a tree which he knew them to attack.

The "garden" was rapidly reconstructed and constantly purified of old pellets. As the garden decreased in size some of the ants set to work upon the leaves, and he was able to watch them, step by step, cut slices from the leaves and tear, chew, and pound these up and finally work them into a pellet which they added to the "garden." It took an ant a quarter of an hour to prepare such a pellet. After the pellets have been inserted into the garden it is perfectly wonderful how quickly it becomes interwoven by fungal threads from neighbouring pellets. Pieces of leaves which had been cut and pounded up in the morning were already interwoven by the fungus in the afternoon.

By these experiments Möller was able to substantiate the hypothesis of Belt and to clear up in every particular the wonderful operations that proceed within the nest.

Moreover, further observations showed Möller that there were special "gardener" ants living within the nest. These ceaselessly weeded the garden so that no foreign fungus or bacterium could spring up. Only those who have attempted to keep a culture of any fungus pure realise the difficulty of doing so. The spores of the various moulds and bacteria are omnipresent, and a single unguarded moment suffices for these to enter the culture and render it impure. Nevertheless, in the face of all these difficulties the ant-gardeners succeed in growing only the one fungus which serves them for food and eliminating all other organisms. If a piece of "garden" is kept in the glass basin with only a very few of these gardener-ants the threads of the fungus begin to grow out into the air. The ants at once "prune" these aerial branches off; but as so few ants are present they cannot work quickly enough, and before long such a forest of fungal air-threads have grown up that the ants can no longer move through the dense jungle.

What we have learnt, therefore, of these leaf-cutting ants is that some travel far afield from their homes to fetch leaf-fragments, which are specially prepared and worked up into a "bed" upon which a special fungus can grow; that other ants are road-menders, repairing and overseeing the paths along which the leaf-cutters must travel; whilst other workers stay within the nest as "gardeners," who weed the fungus-beds and prune the plants which they have in their charge.

The following pages of Möller's book are of the highest importance to the special student of Fungi, but we must hurry over them with a mere reference. He succeeded in growing the fungus of the ant-garden in artificial cultures, and he discovered that several secondary fruit-forms were developed by this plant. Moreover, he was able to induce it to produce the "Kohlrabi-heaps," which are the special food of the ants. These Kohlrabi-heaps are formed by the ends of the threads, which swell up into little round bladder-like structures filled with protoplasm. Another important discovery was that of the primary fruit-form, which showed the fungus to belong to the Agarics (to which the mushroom and toadstools also belong). The

genus under which it must be classified is that of *Rozites*, and Möller names the fungus *Rozites gongylophora*.

Möller concludes his work with a description of the fungal-gardens of two other genera of ants—the Hairy-Ant (*Apterostigma*) and the Hillock-Ant (*Cyphomyrmex*), but I have no time to say anything of these, except that they are both "gardeners," but neither leaf-cutters. They build their nests in rotten wood and construct their "gardens" of the wood-meal and excrements formed by insects (beetle-larvæ, etc.) which burrow in the decayed wood.

In an earlier part of this paper I have attempted to make clear to you the enormous damage that these leaf-cutting ants can work upon the surrounding vegetation. It now remains for us to enquire why it is that certain plants remain untouched by these ants, whilst others are entirely destroyed by them.

In some cases it is the oily or resinous secretions* contained in the plant which gives them immunity from the leaf-cutting ants, but there are other plants which have no such secretions and in which the leaves appear most suitable for "cutting," but which are, nevertheless, untroubled by these pests of the tropics.

Before we can understand the reason for this immunity enjoyed by certain species of plants it must be pointed out that the leaf-cutters are not the only kind of ant inhabiting these countries. There are as well other genera, many of which are distinguished by their warlike habits.

Bates, in his delightful book, "The Naturalist on the River Amazon," has described the triumphant progress of an army of ants belonging to the genus *Eciton*. The approach of a column of these ants is heralded by the restless flight of birds. As soon as an Indian sees these birds he takes to his heels, but the less wary European, not understanding the meaning of these signs, will probably be overtaken by the ants, which will cover his body in thousands, and, fixing themselves to his skin with their mandibles, will sting him from head to foot. Every caterpillar, or spider, or other ant which falls across the path of these fierce warriors is immediately set upon. They will attack a wasps' nest without the least hesitation, and, tearing it to pieces, will drag out the soft larvæ quite regardless of the furious insects which buzz around them.

It is a very old observation that some genera of these fighting ants inhabit hollow cavities in certain species of plants. Thus, as long ago as 1688 John Ray found the hollow stem of *Cecropia palmata* inhabited by ants. In 1763 Jacquin related that when a bush of Acacia was touched an army of furious ants rushed out from its interior. In 1750 Rumphius found the tubers of *Hydnophytum* and *Myrmecodia* to contain warlike ants. It was Thomas Belt, however, who first interpreted these facts correctly. After describing certain points in the structure of *Acacia cornigera* he concludes by saying: "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."

Many have studied this subject since Belt's time, but they all confirm his conclusion, and the work of Schimper, perhaps more than that of anyone else, has finally and conclusively shown that the immunity which certain plants possess from the leaf-cutting ant is due to the presence of warrior-ants in their interior who drive off any leaf-cutter who attempts to set foot upon the plant.*

One of the earliest known and most thoroughly studied cases of plant-hospitality towards their soldier guests is that of the Trumpet-tree (*Cecropia*).

If one of these trees is somewhat roughly handled an army of ants rushes out from little holes in the stem and fiercely attacks the aggressor. The ants inhabiting *Cecropia adenopus* always belong to the same species, *Azteca instabilis*, and they are among the most warlike of the ants to be met with in Brazil. A tree provided with an army of Azteca ants is never touched by the leaf-cutting ants.†

In those rare cases, however, in which for some reason or other the tree is left without its soldier-guests, the leaf-cutters at once set to work on its leaves and very quickly demolish them. In exchange for the very valuable service that the Azteca ants perform for the Trumpet-tree this provides the ants both with shelter and with food. The stems of *Cecropia* are hollow and partitioned up into little chambers by very thin diaphragms. Each of these diaphragms is bitten through by the ant, so that all the chambers communicate with one another.

Above the place at which a leaf is inserted on the stem a specially thin spot, composed of only soft tissues, is left. This thin region is easily perforated by the ant, which is thus furnished with a door into its abode above every leaf.

At the base of each leaf stalk is a patch of brown, velvet-like hairs, between which curious little white, egg-shaped bodies lie. These little bodies were first noticed by Fritz Müller, and are called after him "Müller's bodies."

They form the staple food of the ants, and, consisting of soft parenchyma-cells rich in proteids and fatty matters, they are no doubt highly nutritious.‡

The Acacias are, for the most part, prickly shrubs or small trees. Usually the prickles are small and solid, but in some instances they are both large and hollow.

When this is the case the prickles are nearly always inhabited by ants. *Acacia sphærocephala* (Willd.) is a not uncommon bush in Mexico, Central America, and the Greater Antilles. The relation of this shrub to ants was first described by Thomas Belt.

"The thorns of the bull's horn Acacia," he writes, "are hollow, and are tenanted by ants that make a small hole for their entrance and exit near one end of the thorn, and also burrow through the partition that separates the two horns, so that one entrance serves for both. Here they rear their young, and in the wet season everyone of the thorns is tenanted, and hundreds of ants are to be seen running about, especially over the younger leaves. If one of them be touched, or a branch shaken, the little ants (*Pseudomyrma bicolor*, Guer.) swarm out from the hollow thorns and attack the aggressor with jaws and sting. They sting severely, raising a little white lump that does not disappear in less than twenty-four hours. They form a most efficient standing army for the plant, which prevents not only the mammalia from browsing on the leaves, but delivers it from the attacks of a much more dangerous animal—the leaf-cutting ant. For these

* The smooth, waxy surfaces of the stems of some plants afford no foot-hold to the ants, and are thus protected.

* See Addendum at conclusion of this Article.

† In very cold periods the soldier ants are benumbed and can no longer defend the tree against the leaf-cutters, which stand the cold much better, and are still active at comparatively low temperatures.

‡ For a fuller account of Cecropia, see especially (1) Fritz Müller's paper in Kosmos, Bd 8, 1880, and (2) Schimper's "Die Wechselbeziehungen Zwischen Pflanzen und Ameisen," Jena, 1888.

services the ants are not only securely housed by the plant, but are provided with a bountiful supply of food, and to secure their attendance at the right time and place the food is so arranged and distributed as to effect that object with wonderful perfection."

Again he writes: "These ants seem at first sight to lead the happiest of existences. Protected by their stings they fear no foe. Habitations full of food are provided for them to commence housekeeping with, and cups of nectar and luscious fruits await them every day. But there is a reverse to the picture. In the dry season on the plains the Acacias cease to grow. No young leaves are produced, and the old glands do not secrete honey. Then want and hunger overtake the ants that have revelled in luxury all the wet season; many of the thorns are depopulated, and only a few ants live through the season of scarcity. As soon, however, as the first rains set in, the trees throw out numerous vigorous shoots, and the ants multiply again with astonishing rapidity."

I have quoted at length from the pages of Belt's "Naturalist in Nicaragua" because no words can better express the case for Acacia than these of the original discoverer. The nectar which the plant provides for its guests is formed in little cup-shaped glands situated upon the stalk to which the leaflets of the compound leaf are attached.

The food which the Acacia offers to its defenders consists of curious little pear-shaped, orange-yellow bodies —called Belt's bodies—which grow from the tips of the leaflets.

The researches of Francis Darwin* have shown that both the Belt's bodies of Acacia and the Müller's bodies of Cecropia are special modifications of ordinary leaf-glands, and it is certainly remarkable that two plants so widely separated from one another systematically should show such similar adaptations.

The most recent addition to the list of plants which afford board and lodgings to a defensive army of ants is *Macaranga triloba*, which has been studied by Miss Winifred Smith. This plant, which belongs to the Euphorbiaceæ, was found growing in the neighbourhood of Singapore. Its stems are hollow and divided into chambers by a series of diaphragms, which, however, become perforated. Ingress and egress into the cavity of the stem is afforded by little holes which are bored through the walls of the stem along a groove of thin tissue that extends above the point of leaf-insertion.

* F. Darwin, "Journal of Linnean Soc.," Vol. XV.

At the base of each leaf-stalk are a pair of curiously-shaped stipules which are pressed against the stem. Over the concave surface of these stipules are arranged a number of little, pear-shaped or spherical, golden-yellow food-bodies comparable with the Beltian or Müllerian corpuscles to which we have already referred.

The tips of the teeth along the margin of the leaf are converted into little cup-shaped glands which secrete nectar, no doubt for the benefit of the ant.

In the hollow stem Miss Smith found not only adult ants, but also pupæ and larvæ. These ants have been identified by Colonel Bingham as belonging to an apparently undescribed species of *Cremastogaster* near *C. daisyi* (Forel).†

Two very strange-looking plants from the Malay Archipelago—*Myrmecodia* and *Hydnophytum*—afford a home to certain ants, but do not provide them with food. These plants carry on an epiphytic existence upon tree trunks, and, as an adaptation to such a dry and airy situation, they have developed enormous tuberous water reservoirs.

These water reservoirs are not solid throughout, but their interior is channelled in every direction with communicating passages. These passages are very probably connected with the aeration of the tissues of the tuber. Certain warlike red ants bore their way into these tubers and find the system of air passages a very comfortable home in which to live and bring up their young. A touch upon one of these plants thus inhabited will serve to bring forth an army of defenders ready to drive away the intruder.

Many other cases of what I have called "plant-hotels" have been studied, but, interesting as these all are, it would take too long to describe them. The cases which I have selected are, I think, representative, and will serve to illustrate the general features of these remarkable phenomena which are the common property of the two sciences of Botany and Entomology.

Since the above article was written papers have appeared from the pens of Ihering, Rettig, Ule, and Nieuwenhuis-Uexküll in which certain of Schimper's conclusions are questioned. It is impossible to discuss these papers here, but they show that the last word has not yet been said with regard to the relations existing between plants and ants.—R. B.

† For a full account of this case, see Miss Winifred Smith's paper "Macaranga Triloba: A New Myrmecophilous Plant," The New Phytologist, Vol. II., May, 1903, p. 79.

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Inside every nest, wherever + however built, there is always a loose, soft, grey, flocculent porous mass which is channeled + ~~hollowed~~ like a sponge. This mass has been called "ant-food" by Thomas Belt + the "Pilzgarten" by Möller. I will call it the ant-garden in the present paper. ×

The ant-garden contains the eggs, larvae & pupae of the ants in its pores + passages; it is always free from the walls of the nest but is never found uncovered. Atta coronata usually builds its nests underground & not infrequently it bores for more than a yard below the surface before it constructs its "garden".

The nests of Atta IV are similar to those of A. disciger but on a smaller scale. If a fragment of the ant-garden be broken off & examined under a lens it will be seen to be composed of numberless little soft ~~green~~ pellets each about $\frac{1}{50}$" of an inch in diameter. These pellets when they are quite fresh are dark green, older ones are almost black whilst very old ones are yellow-brown in colour. They are interwoven with the threads of a fungus & it is these threads which take the place of mortar & bind the pellets together into the mass of the ant-garden. Spread over the entire surface of the "garden" are an enormous number of little, round, white bodies varying from between $\frac{1}{50}$" & a $\frac{1}{100}$" of an inch in diameter. (2) Möller has called these the "Kohlrabi-heaps" These "Kohlrabi-heaps" are part & parcel of the fungus which interweaves the pellets of the garden

& under the microscope are seen to be little round swellings upon the superficial threads of the fungus. X

As was pointed out at the beginning of this paper it has been well known for many years that these ants cut & carry fragments of leaves to their nests. The number of leaf-fragments which thus reach the nest is very large: Müller observed 214 loaded ants to pass one point on the path leading to the nest in a quarter of an hour & Belt, in Nicaragua, the number of ants which move along the tracks is far greater. In spite of this no leaf-fragments accumulate in the nest itself & their fate has been the subject of much wonder & surmise to many naturalists. Some have believed that the ants eat the pieces of leaf, others imagined that the nest was built of these fragments & finally Thomas Belt hazarded a guess of the most sensational character as to the uses which was made of the pieces of leaf.

He believed that the leaf-cutting ants were gardeners & that they ~~prepared~~ actually prepared beds with the leaf-fragments that they brought to the nest & that upon these they grew a fungus for their food. "I believe" he writes "that they are in reality mushroom growers & eaters."

Belt's supposition was of so remarkable a character & ~~was~~ so ~~supported~~ he was able to bring forward so few facts to support it that although it attracted a great deal of attention it found but few adherents.

Möller, armed with the resources of a splendidly equiped laboratory, ~~was able~~ attacked the problem with an ingenuity of mind & an untiring enthusiasm which must win for him our highest admiration.

That the ant-garden is greatly valued by the ants is shown by the scrupulous care with which they gather up every fragment of a "garden" that has been removed from a nest & scattered on

the ground. If a nest is several times disturbed its inhabitants will desert it & make their home elsewhere. When this is done however, they carry with them, not only their eggs & larvae, but every morsel of the "garden". Miller next examined the ~~f~~ ant-garden microscopically & he was able to ~~make out~~ ascertain that the pellets of which it is built consists of torn ~~blue~~ shreds of leaf. Stomata, epidermal cells, & chloroplyll grains could all be seen in these pellets. There was ^ strong reason to believe, therefore, that some, if not all the pieces of leaves ~~which~~ which are carried to the nest are shredded out & worked up into these ^ tiny little soft building - stones of the garden.

The next step which Miller took was the attempt to ~~glass~~ keep the ants in captivity under such conditions that he could ~~watch~~ constantly watch their operations.

After many failures he at last succeeded in this attempt.

In a covered glass ~~bas~~ basin he placed a few workers of Atta disciçera or A. hystrix & after crumbling up a piece of "garden" to tiny pieces he scattered these over the bottom of the basin. The ants at once set to work at the pieces of garden & within 12 hours they had reconstructed a new garden. All bits of dirt or other foreign matter were carefully separated & set on one side.

Continuing his observations on the following days Möller noticed that the older pellets, upon which the fungus no longer grew were removed from the garden & added to the heap (or rather layer) of refuse. As this went on the nest becomes smaller & smaller until at last nothing is left of it. The ants then run aimlessly about & after 8 to 14 days they are all dead. From this it is seen that the ~~so~~ life of the ant is bound up with the existence of the "garden"

In another experiment a little moist Sand was placed in the glass vessel, a few leaves of a plant the ants usually "cut", & a certain number of ants. The ants burrowed into the Sand but never touched the leaves. After some days Starvation a small fragment of fungus garden was introduced into the basin. An ant mowed to it & after scenting it hastened under the Sand to return almost at once accompanied by ten other ants. These all hurried to the "garden" & beginning them under a magnifying glass, Müller could see that they greedily tore off & devoured the Kohlrabi-heaps of the fungus. Again Müller starved ants for several days & then presented them with the Kohlrabi-heaps of the fungus upon the end of a needle. These they at once seized & ate.

Finally Müller kept a number of ants in a glass basin together with the fragments of a "garden" & several leaves from a tree which they were accustomed to. He knew them to attack

The "garden" was rapidly reconstructed & constantly purified of old pellets. As the garden decreased in size some of the ~~workers~~ ants set to work upon the leaves & he was able to watch them, step by step, cut ~~the leaves~~ slices from the leaves & tear, chew & pound these up & finally work them into a pellet which they added to the "garden". It took an ant a quarter of an hour to prepare such a pellet. After the pellets have been inserted into the garden it is perfectly wonderful how quickly it becomes interwoven by fungal threads from neighboring pellets. Pieces of leaves which had been cut & pounded up in the morning were already interwoven by the fungus in the afternoon.

By these experiments Müller was able to substantiate the hypothesis of Belt & to clear up in every particular the wonderful operations that proceed within the nest.

Moreover, further observations showed Müller that there were special "gardener" ants living within the nest. These ceaselessly weeded the garden so that no ~~fungi~~ foreign fungus, or bacterium could spring up. Only those who have attempted to keep a culture of any fungus pure ~~from~~ realize the difficulty of doing so. The spores of the various moulds & bacteria are omnipresent & a single unguarded moment suffices for them to enter the culture & render it impure. In the face of all these difficulties the ant-gardeners succeed in growing only the one fungus which serves them for food & eliminating all other organisms. If a piece of "garden" is kept in the glass basin with only a very few of these gardener-ants the threads of the fungus begin to grow out into the air. The ants at once "prune" these aerial branches off; but as so few ants are present they cannot work quickly enough & before long such a forest of fungal air-threads have grown up that the ants can no longer more

through the dense jungle.

What we have learnt, therefore, of these leaf-cutting ants is that some travel far afield from their homes to fetch ~~food~~ leaf-fragments which ~~others~~ + that these are specially prepared + worked up into a "bed" upon which a special fungus can grow; that other ants are road-menders, repairing + overseeing the paths along which the leaf-cutters must travel; whilst other workers stay within the nest as gardeners who weed ~~+ prune~~ the fungus-bed + prune the plants which they have in their charge.

The following pages of Müller's book are ~~perhaps the~~ of the highest importance to the special student of Fungi but we must hurry over them with a mere reference.

He succeeded in growing the fungus of the ant-garden in artificial cultures + he discovered that several secondary fruit-forms were developed by this plant. Moreover he was able to

induce it to ~~to~~ produce the "Kohlrabi-heaps" which are the special food of the ants. These Kohl-rabi-heaps are ~~the~~ formed by the ends of the threads which swell up into little round bladder-like structures filled with protoplasm. Another important discovery was that of the primary fruit-form which showed the fungus to belong to the Agarics (to which the mushroom + toadstools also belong). The genus of under which it must be classified is that of Rozites. Möller names the fungus Rozites gongylophora. ×

Möller concludes his work with ~~be~~ a description of the fungal-gardens of two other genera of ants — the Hairy-Ant (Apterostigma) + the Hillock-Ant (Cyphomyrmex) but I have no time to say anything of these except that they are both "gardeners" but neither leaf-cutters. They build their nests in rotten wood + construct their "gardens" of the wood-meal + excrements ~~of the~~ formed by insects (beetle-larvae etc) which burrow in the decayed wood.

In an earlier part of this paper I have attempted to ~~show~~ make clear to you the enormous damage that these leaf-cutting ants can work upon the surrounding Vegetation. It now remains for us to Enquire why it is that certain plants remain untouched by these ants whilst others are entirely destroyed by them.
In some cases it is the oily or resinous secretions(1) contained in the plant which gives them immunity from the leaf-cutting ants but there are other plants which have no such secretions + in which the leaves appear most suitable for "cutting" but which are nevertheless untroubled by these pests of the tropics.
Before we can understand the reason for this immunity enjoyed by certain species of plants it must be pointed out that the leaf-cutters are not the only kind of ant inhabiting these countries. There are as well many other genera, many of which are easily distinguished by their warlike habits.

(1) The # smooth waxy surfaces of the stems of some plants afford no foot hold to the ants + are thus protected.

Bates, in his delightful book "The Naturalist on the river Amazon" has described the triumphant progress of an army of ants belonging to the genus Eciton. ~~It only~~ The approach of a column of these ants is heralded by the restless flight of birds. As soon as an Indian sees these birds he takes to his heels but the less wary European, not understanding the ~~significance~~ meaning of these signs will probably be overtaken by the ants which will cover his body in thousands, ~~& bite him with their pincers & fangs from head to foot~~ &, fixing themselves to his skin with their mandibles, will sting him from head to foot. Every caterpillar, or spider or other ant ~~of another kind~~ which falls across the path of these fierce warriors is immediately set upon. They will attack a wasp's nest without the least hesitation & tearing it to pieces will drag out the soft larvae quite regardless of the furious insects which buzz around them

It is a very old observation that some genera of these fighting ants inhabit hollow cavities in certain species of plants. Thus as long ago as 1688 John Ray found the hollow stem of Cecropia palmata inhabited by ants. In 1763 Jacquin related that when a bush of Acacia was touched an army of furious ants rushes out from its interior. In 1750 Rumphius found the tubers of Hydnophytum & Myrmecodia to contain warlike ants. It was Thomas Belt, however, who first interpreted these facts correctly. After describing certain points in the structure of Acacia cornigera he concludes by saying: "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 & insects".

Many have studied this subject since Belt's time but they all confirm his conclusion &

the work of Schimper, perhaps more than that of any one else has finally & conclusively shown that the immunity which certain plants possess from the leaf-cutting ant is due to the presence of warrior-ants in their interior ~~or that~~ who drive off any leaf-cutter who attempts to set foot upon the plant.

One of the earliest known & most thoroughly studied cases of plant-hospitality towards their soldier-guests is that of the Trumpet-tree — Cecropia —. ×

If one of these trees is somewhat roughly handled an army of ants rushes out from little holes in the stem & fiercly attacks the aggressor. The ants inhabiting Cecropia adenopus always belong to the same species — Azteca instabilis — & they are among the most ~~world~~ warlike of the ants to be met with in Brazil. A tree provided with an army of Azteca ants is never touched by the leaf-cutting ants.(1) In those rare cases, however, in which for some

(1) In very cold periods the soldier ants are benumbed & can no longer defend the tree against the leaf-cutters which stand the cold much better & are still active at comparatively low temperatures.

reason or other the tree is left without its Soldier-guests the leaf-cutters at once set to work on its leaves & very quickly demolish them. In exchange for the very valuable service that the Azteca ants perform for the Trumpet tree this provides the ants both with ~~a home in which~~ shelter & with food. The stems of Cecropia are hollow & partitioned up into little chambers by very thin diaphragms. Each of these diaphragms is bitten through ~~by the ants~~ by the ant so that all the chambers communicate with one another. X Above the ~~place~~ ~~spot~~ at which a leaf is inserted on the stem a specially thin spot, ~~with a~~ composed of only soft tissues, is left. This thin region is easily perforated by the ant which ~~is~~ is then furnished with a door into its abode above every leaf. X At the base of each leaf stalk is a patch of brown, velvet-like hairs between which curious little white, egg-shaped bodies lie. These little

bodies were first noticed by Fritz Müller & are called after him "Müllers-bodies". They form the stable food of the ants, consisting of soft parenchyma-cells rich in proteids & fatty matters, they are no doubt highly nutritious.(1)

The Acacias are for the most part prickly shrubs or small trees. Usually the prickles are small & solid but in some cases they are both large & hollow. When this is the case the prickles are nearly always inhabited by ants.

Acacia Sphaerocephala (Willd.) is a not uncommon bush in Mexico, Central America & the Greater Antilles. The relation of this shrub to ants was first described by Thomas Belt. "The thorns of the bull's horn Acacia" he writes "are hollow, & are tenanted by ants that make "a small hole for their entrance & exit near "one end of the thorn, & also burrow through "the partition that separates the two horns, so that "one entrance serves for both. Here they rear

(1) For a fuller account of Cecropia see especially (1) Fritz Müller's paper in Kosmos Bd 8 1880 & (2) Schimper's "Die Wechselbeziehungen zwischen Pflanzen & Ameisen" Jena 1888.

"their young, + in the wet season every one of the
"thorns is tenanted, + hundreds of ants are to be seen
"running about, especially over the younger
"leaves. If one of them be touched, or
"a branch shaken, the little ants (Pseudomyrma
"bicolor Guer.) swarm out from the hollow
"thorns, + attack the aggressor with jaws
"+ sting. They sting severely, raising a
"little white lump that does not disappear in
"less than twenty-four hours. They form a
most efficient standing army for the plant,
"which protects not only the mammalia from
"browsing on the leaves, but delivers it from
"the attacks of a much more dangerous
"animal — the leaf-cutting ant. For these
"services the ants are not only securely housed
"by the plant, but are provided with a
"bountiful supply of food, + to secure their
"attendance at the right time + place, the
"food is so arranged + distributed as to
"effect that object with wonderful perfection"

Again he writes" These ants seem at first
"sight to lead the happiest of existences.
"Protected by their stings, they fear no foe.
"Habitations full of food are provided for
"them to commence housekeeping with, & cups
"of nectar & luscious fruits await them
"every day. But there is a reverse to the
"picture. In the dry season on the plains
"the acacias cease to grow. No young leaves
"are produced, & the old glands do not
secrete honey. Then want & hunger
"overtake the ants that have revelled in
"luxury all the wet season; many of the
"thorns are depopulated, & only a few of the
"ants live through the season of scarcity. As
"soon, however, as the first rains set in, the
"trees throw out numerous vigorous shoots, &
"the ants multiply again with astonishing
"rapidity"

I have quoted at length from the pages of Belt's "Naturalist in Nicaragua" because

No words can better express the case for Acacia than those of the original discoverer. "The nectar which the plant provides for its guests is formed in little cup-shaped ~~glands upon the rachis of the compound leaf (pinna doubly pinnate)~~ glands situated upon the stalk to which the leaflets of the compound leaf are attached. The food which the Acacia offers to its defenders consists of curious little, pear-shaped orange-yellow bodies called Belt's bodies which grow from the tips of the leaflets. The researches of Francis Darwin[1] have shown that both the Belt's bodies of Acacia & the Müller's bodies of Cecropia are specially modified leaf-glands ~~Special modifications of ordinary leaf-glands~~ & it is certainly remarkable that two plants so widely separated from one another by systematists should show such similar adaptions.

(1) F. Darwin Journal of Linnean Soc. Vol XV

The most recent addition to the list of plants which afford board + lodgings to a defensive army of ants is Macaranga triloba which has been studied by Miss Winifred Smith. This plant, which belongs to the Euphorbiaceæ was found growing in the neighbourhood of Singapore. Its stems are hollow + divided into chambers by a series of diaphragms which, however, become perforated. Ingress + egress into the cavity of the stem is afforded by little holes which are bored through the walls of the stem along a groove of their tissue that extends above the point of leaf-insertion. At the base of each leaf-stalk are a pair of curiously shaped stipules which are pressed against the stem. On the concave surface of these stipules are arranged a number of little, pear-shaped or spherical, golden-yellow food-bodies comparable with the Beltian or Müllerian corpuscles to which we have already referred.

The tips of the teeth along the margin of the leaf are converted into little cup-shaped glands which secrete nectar, no doubt for the benefit of the ant.

In the hollow stem Miss Smith found, not only adult ants, but also pupae & larvae. These ants have been identified by Colonel Bingham as belonging to an apparently undescribed species of Cremastogaster near C. daisyi (Forel).[1]

Two very strange looking plants from the Malay Archipelago — Myrmecodia & Hydnophytum — afford a home to certain ants but do not provide them with food. These plants carry on an epiphytic existence upon tree-trunks &, as an adaption to such a dry & airy situation, they have developed enormous, tuberous ~~water-reservoirs~~ water-reservoirs.

[1] For a full account of this case see Miss Winifred Smith's paper "Macaranga Triloba: A new Myrmecophilous Plant" The New Phytologist Vol II May 1903 p. 79.

These water reservoirs are not solid throughout but ~~are channeled~~ their interior is channeled in every direction with communicating passages. These passages are very probably connected with the aeration of the tissues of the tuber. Certain warlike red ants bore ~~their way~~ their way into these tubers & find the system of air-passages a very comfortable home in which to ~~bring up~~ their ~~young~~ live & bring up their young. A touch upon one of these plants, thus inhabited, will seem to bring forth an army of defenders ready to drive away the intruder.

Many other cases of what I have called "plant-hotels" have been studied but, interesting as these all are, it would take too long to describe them. The cases which I have selected are, I think, representative, & will serve to illustrate the general

features of these remarkable phenomena which are the common property of the two sciences of Botany & Entomology.

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