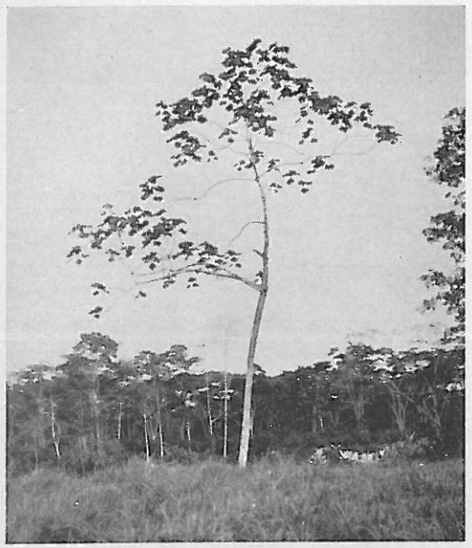
# THE MOST HOSPITABLE TREE

By ALEXANDER F. SKUTCH

WHILE yet an undergraduate in college, I was familiar with that remarkable work *Botanische Mittheilungen aus den Tropen.* In the nine slender volumes of this beautifully illustrated series of monographs, edited and in part written by the famous plant geographer A. F. W. Schimper, and published during the years 1888 to 1901, I became acquainted with some of the most fascinating phenomena of tropical botany: the adaptations of epiphytic plants, the strange modes of secondary thickening in the stems of woody vines, the complex relationships between ants and the plants that provide shelter for them, the fungus gardens of the leaf-cutting ants. Perhaps no other single work so strongly influenced my determination to devote some years to the firsthand study of tropical Nature—years that have stretched on and on to nearly two decades.

To the young student of Nature in the first exhilaration of his studies, no Sir John Mandeville or Marco Polo had filled his pages with more wonder-stories than were to be found in these records of sober scientific investigation. And perhaps the most marvelous of all the volumes, both in the patent drama of the situation described and in the agelong series of delicate adjustments and readjustments between organisms implied in the relationship, was the monograph by Schimper himself, on the Cecropia tree and its garrison of ants. Widely traveled, enthusiastic, keen-sighted, endowed in no small degree with the capacity for "the scientific use of the imagination," the author pointed out the features that made the tree a most favorable abode for the ants, providing them not only with commodious lodgings but also with a special and delicate food. In return for food and housing, the hordes of little biting ants defended the tree against its enemies. Such, in brief, was Schimper's thesis, which, during many years' residence and travel in widely separated portions of the range of the Cecropia tree, I have had constantly in the back of my mind, so that observations, made deliberately or by chance, were classified according to whether they confirmed or refuted it. Will this story, which stirred the imagination of the young student, stand the test of a far longer familiarity with the Cecropia tree than its author himself enjoyed?

When at length I reached the Tropics, I was not long in recognizing the tree whose remarkable history I knew so well. Indeed, the genus *Cecropia,* of the mulberry family, contains the most distinctive trees of the New World Tropics. It comprises thirty to forty species, distributed not only over the entire length and breadth of the intertropical areas of the American continents but in the Antilles and other outlying islands as well. Were a wizard to drop a naturalist at random, blindfolded, somewhere within the vast sweep of the earth's central zone, no other single group of trees would so help him decide, by their presence or absence, whether he had been set down in the Western or the Eastern Hemisphere. For over its vast range, there is hardly a district with heavy or moderate rainfall where it is not abundant. It is absent only from desert and semidesert areas and from high mountains subject to nocturnal frosts. Yet in the equatorial Andes it grows abundantly up to an elevation of at least 8,500 feet, and in Central America to no less than 6,000 feet. Most common in the clearings and light second-



CECROPIA TREE, PANAMA

growth woodland, where frequently it is the dominant tree, it is by no means absent from primeval forest, often springing up in the little, light-flooded clear spaces left by the fall of a forest giant. Almost everywhere it is recognized and named by the country people. Throughout Central America it is called *guarumo;* in the montaña of Peru, *setico;* in the British West Indies, *trumpet tree.*

Not only wide range and abundance but also the ease with which the veriest novice in the forest can recognize them entitle the Cecropias to be considered the most characteristic trees of tropical America. In tropical forests, the leaf shape of scores and hundreds of kinds of trees is monotonous in the extreme—very different from the attractive variety of outline of the foliage of the oaks, maples, beeches, and chestnuts of a northern forest. Flowers are usually high out of reach, often inconspicuous, and to be had only at certain seasons and by the most adept climber; color and texture of bark sometimes lead the practiced eye to a correct identification, but they are not always to be relied upon. Familiarity with the trees of the tropical forest is to be gained only by long and arduous collecting, patient research, and much taxonomic skill. There are probably not ten men alive who could correctly name at sight half the species of trees in an acre of well-developed virgin forest anywhere in the tropical lowlands of the American continents. How refreshing, then, to find a tree so distinct from all its neighbors, in foliage, bark, form, and half a dozen other well-marked characters that there is scarcely any possibility of confusion! Any intelligent lad from some far northern land, sent with only a written description to a tropical forest and told to bring back a specimen of a Cecropia tree, should be able to pick it out unaided and at first sight. I know no other tree of the tropical American forests for which I would hazard the same statement.

The Cecropias are small, medium-sized, or rarely (for the Tropics) tall trees, never attaining the height of the giants of the forest, nor ever remotely approaching them in the girth of their slender, graceful trunks. The bark is smooth, light gray, whitish, or greenish in color and prominently ringed, at intervals of a few inches, with narrow ridges—scars left by the fallen bud-sheaths. This smooth, light-colored, strongly ringed trunk alone serves to distinguish the Cecropia from nearly all its neighbors. At its very base, where it nears the ground, the trunk becomes slenderer instead of thicker; and the deficiency in girth and strength is counterbalanced by the presence of numerous prop roots, sometimes springing from the bole as high as 4 or 5 feet above the earth and descending obliquely until they enter the soil and ramify through it. Prop roots are not peculiar to the Cecropia—many other dicotyledonous trees, many palms, the pandanus, and even the maize plant have them—yet they will distinguish it from the vast majority of the trees among which it grows. The boughs of the Cecropia are coarse, stiff, and few in number, the lowest branches usually springing from the bole well above the ground. The branches are distributed in loose clusters, or false whorls, three to six together, with long stretches of branchless trunk between successive clusters. Like the trunk, the obliquely ascending boughs diminish little in thickness from base to top, and they bear few branchlets of the second order.

If the leaves were small, such a branch system would produce a stiff and awkward tree; but on a well-developed Cecropia all suggestion of stiffness is prevented by the generous breadth and grace of carriage of the foliage. The ample leaves, sometimes a yard in diameter, are held in a more or less horizontal position at the end of yard-long, rounded stalks. They are peltate, roundish in outline, divided by deep and narrow indentations into long radiating lobes, and in some species silvery on the lower side, presenting a pleasing and characteristic aspect when tossed up by the wind. Rarely, as in *Cecropia araliaefolia* of the eastern foothills of the Andes, the lobing has been developed to the point where the leaves are divided into distinct, stalked leaflets, all radiating from the end of the long common stalk, like those of the horse-chestnut tree.

The flowers, minute and individually inconspicuous, seem unworthy of a tree with such pronounced and individual characters. Yet in their arrangement they too are sufficiently distinctive. They are closely crowded in fingerlike aments, or catkins, in some species short and stubby, in others long and slender, sometimes twisted. These fingers are borne, in clusters of four or more, at the end of a common stalk, which may be short and stiff or long and pendulous. Male and female catkins are produced on separate trees, the former whitish and soon falling, the latter green and persistent, scarcely altering in appearance as their myriad florets swell into tiny one-seeded fruits. Each cluster of aments develops within a close-fitting sheath, which is white within and often has an attractive shade of pink or red on the exterior surface. This sheath splits along one side and drops when the flowers are ready to shed, or to receive, their pollen. It is the most colorful part of the tree.



THE BROAD, MANY-FINGERED FOLIAGE OF THE CECROPIA

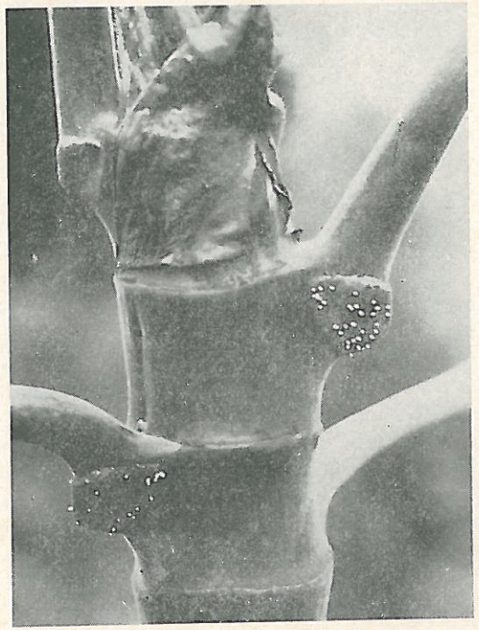
A few words about the ecology of the Cecropia will help us to understand some of its peculiarities of form, especially its system of branching. It is a tree pre-eminently adapted for the colonization of denuded lands, whether these be a new clearing in the forest, an abandoned patch of cultivation, a flood plain along the shifting course of a great river, or the long, narrow band of raw earth streaked upon the mountain side by a landslide. On such areas tropical vegetation wears its most lush, most riotous and undisciplined aspect. The competition among the colonizers is exceedingly keen; the slow-growing seedling, although of the noblest lineage of the forest, has slight chance of success; victory—immediate victory, at least—favors the plant that can keep its "head and shoulders" above its rivals and so enjoy full exposure to the strength-giving sunlight. A wide-spreading, many-branched plant is likely to be smothered over and crushed down by a tangled mat of vines and creepers. The successful tree must not only grow rapidly in height, but it also must be sparing in the matter of breadth, hugging itself together lest it waste much-needed energy in horizontal expansion and give the eager, grasping vines a hold on itself. Such a tree is the Cecropia. Seemingly intent only upon outreaching its competitors, in crowded tangles it may attain a height of 20 or 30 feet, or even more, before it ventures to extend a single branch. Its ample leaves, each of which seems capable of the photosynthetic work of a whole spray of the smaller leaves of a northern plant, fall when their activity is taken over by younger leaves above them, thereby giving the creepers no permanent grasp upon the tree. So great is the heliotropism, or sunward impulse, of the vigorous young Cecropia that its slender stem is commonly dilated upward and, like scarcely any other tree, is thickest at the top, in the succulent green portion just below the apex. The inverted taper of the trunk is corrected in later life, when the tree has won the victory and spread its branches proudly above the rival vegetation, in part by secondary thickening, in part by the development of the stout prop roots at the base.

Such, then, are the appearance and mode of growth of the most highly individualistic tree of the American Tropics. We have already discovered, in its very lineaments and most obvious outward vestiture, enough idiosyncrasies for any one tree. Yet we have scarcely begun to explore its peculiarities. Shake the branches of a Cecropia, and a host of small, brown or blackish ants comes swarming out through narrow, symmetrically placed orifices. They run hastily over bark and leaves and on to any object touching them, each biting with all its small might if it meets the body of an animal. Cut through the young stem or a branch with a single sharp blow of the machete, and the severed end reveals a central hollow, left by the almost complete breakdown of the pith, wider than in any other young woody stem I know. Or stand quietly watching a stem of one of the ant-inhabited species. A keen eye will soon notice that each of the long, hollow leaf stalks is swollen at the base, where it touches the stem, on the lower side, into an angular, kneelike protrusion, which is covered with brown hairs. After years devoted to the collection of tropical plants, handling thousands of species, I can recall no other tree with just such a leaf base. It would be remarkable enough without the little white bodies, each about the size and shape of a small ant's pupa, that stud it over, like little white-headed pins stuck up to the head in a brown velvet pincushion. Watching patiently, one may be fortunate enough to see an ant crawl over the cushion, touching with its antennae one after another of the little white beads, until it finds one that is ripe, plucks it off, and carries it into the hollow center of the branch through one of the small apertures. These, constituting the special food of the ants, are the protein bodies, often called Müllerian corpuscles in honor of their discoverer.

In harboring a colony of ants within its living tissues, the Cecropia is not unique in the vegetable kingdom. It belongs in a motley group known as the myrmecophilous, or ant-loving, plants. Like so many other natural phenomena, the Cecropia can be most intelligently understood if we consider it in relation to the class of objects of which it forms a part.

The myrmecophilous plants have only a single feature in common: the habitual occurrence of colonies of ants in hollow living organs, which, in many instances, appear to have been specially developed for the accommodation of the insects. All or nearly all these plants are of tropical distribution. As a rule a particular species of ant is found in each true myrmecophilous plant—and sometimes the ant is restricted to this peculiar habitat—suggesting that the myrmecophilous habit was developed in relation to this particular kind of guest and that the plant has not merely chanced to produce a hollow organ open to tenancy by the first small insect that happens by. The myrmecophilous plants are scattered sparingly through a considerable number of unrelated families—Rubiaceae, Piperaceae, Moraceae, Boraginaceae, Polygonaceae, Melastomaceae, Verbenaceae, Mimosaceae, etc.—indicating that they are not genetically related, but that the habit has developed independently in many distinct lines. The nature of the organs in which the insects are accommodated is as diverse as the families in which the myrmecophilous plants are classified. Perhaps the most common situation of the ant colony is in a stem left hollow by the breakdown of the central pith. Such ant-filled stems are found, in addition to the Cecropia, in the beautiful *palo santo* (*Triplaris*) and in certain arborescent species of *Piper*. In *Cordia alliodora* the insects find shelter in gall-like hollow nodes, situated at the point where several branches depart together from the end of a thicker twig. In certain tropical melastomes (*Tococa*) they dwell in paired hollow lobes at the base of the leaf blade, each with a narrow orifice on the lower side of the leaf. In some Central American species of *Piper* they establish themselves in the long, narrow hollow formed by stipules that have coalesced with the petiole, thence making their way into the stem and eating out the central pith. In the bull-horn acacias the ant colonies are established in the great, paired, hornlike hollow thorns, from which the curious little trees take their name. The hollows of the paired thorns intercommunicate at their base; and one thorn in each pair is provided by the ants with a small round aperture for going in and out. Perhaps the strangest of all the myrmecophilous plants are two epiphytic genera of the madder family, *Hydnophytum* and *Myrmecodia*, natives of the Indo-Malaysian area, whose curiously swollen stems are penetrated by a labyrinth of winding galleries in which the ants dwell. In eastern Costa Rica I found a species of polypody fern, not yet identified, whose slender stems, creeping over the mossy branches of trees, bear numerous brown gall-like bodies, about an inch in diameter, each with a doorway leading into a central hollow infested by tiny, stinging ants.





APEX OF A CECROPIA SHOOT

CUSHIONS AT PETIOLE BASES SHOWING PROTEIN CORPUSCLES; *left*, GROOVE AND PIT WHERE AZTECA ANTS GNAW; *top*, STIPULAR SHEATH FALLING AWAY.

As a rule the host plant makes no special provision for the board of its lodgers. But in some instances the ants attend aphids that suck the juices of the plant, which thus indirectly provides for the support of its guests. Perhaps the most hospitable of all these myrmecophytes are our Cecropia and the bull-horn acacias, which provide a special food for their guests in the form of small, white protein corpuscles. In the Cecropia these tiny, many-celled corpuscles are, as we have seen, liberally produced, in successive crops, on the cushionlike base of each leaf stalk. In the acacia a single elongate, white food

particle terminates each of the myriad little leaflets of the twice-compound leaf, and once it has been plucked away by the ants that dwell in the hollow thorns at the base of the leaf it is not replaced. The food-bodies of the acacia are sometimes called Beltian corpuscles, in honor of Thomas Belt, who first made them known to naturalists, just as Fritz Müller first described those of the Cecropia.

Of the ants regularly associated with these myrmecophilous plants, some are fierce and aggressive; but many are among the smallest, weakest, most defenseless and sluggish of their kind. They rarely if ever devour the foliage of their host plant or make indiscriminate attacks upon its living tissues. Some botanists believe that these ants benefit the plants in which they find shelter, by driving away foliage-eating insects, browsing mammals, and other enemies of vegetation. If this view be correct, the association between ant and plant is one of mutual benefit; the plant provides a lodging and sometimes also food for the ant, which in turn protects its host from attack. How true this is in the case of the Cecropia we shall now examine.

Of all ant-plants, except possibly the epiphytic myrmecophilous members of the madder family, which I have never seen in their native haunts in the Oriental Tropics, the Cecropia appears to be the most highly specialized. In other words, it *seems* to have made a greater effort to attract its ant guests than any other of the ant-loving plants. Three unique features make it especially favorable as an abode of ants:

1. A remarkably wide central hollow in the stem. Hollow stems are commoner in herbaceous than in woody plants; but except the bamboos no other plant I know possesses, in undecayed young shoots, a central cavity so wide as this. Vigorous shoots often have a cavity fully two inches in diameter—surrounded by walls only about one-sixteenth of an inch thick—and this is to be found only a few inches below the growing tip of the shoot. With age the tissues immediately surrounding the cavity become hard and resistant. When old fallen trunks decay away, this is the last part of them to disappear. The hollow internodes, with their enclosing walls and transverse partitions, remain lying on the ground like a chain of whitish, elongated, cylindrical boxes, or like the bleaching vertebrae of some huge ribless serpent.

2. The presence, in the wall surrounding the hollow that occupies each internode, of a pit, where the ants find it particularly easy to open a doorway. At the upper end of each of the short internodes, directly above the point of insertion of the leaf next below, is the small, somewhat elongate depression. The tissues separating the bottom of this pit from the central hollow are even thinner than the wall elsewhere; and they are composed of soft, thin-walled cells, vascular bundles being absent here. The ants find it easy to gnaw through the bottom of these pits; and in a tree inhabited by a flourishing colony, each one becomes the site of a doorway through which the insects pass in and out. Schimper laid special stress upon these pits, pointing out that they were present in the species of Cecropia habitually infested by ants but absent from those that had not developed the myrmecophilous habit. Similar pits are said to occur in the walls of hollow-stemmed plants of other genera not inhabited by ants, but they are certainly very rare. I have never seen any plant other than Cecropia with such pits.

3. The protein grains at the bases of the leaf stalks. Although such corpuscles, which are of the nature of glands, occur on other plants, some not ant-plants, they are very rare. The only other plants upon which I have seen similar protein corpuscles are the bull-horn acacias, with their hollow thorns inhabited by fiercely stinging ants. In the Old World Tropics they are said to be found on *Pterospermum javanicum,* where they are produced in tiny pitchers at the bases of the leaves; and on the long shoots of climbing species of *Gnetum,* which apparently do not attract ants.

Here, associated in the same tree, are three features—exceptionally wide central hollow, pits, and protein bodies—that although not unknown in plants not myrmecophilous are so rare that one might botanize through the Tropics for months or even years without finding—apart from Cecropia—any one of them singly. What, then, are the chances for a *random* association of the three in the same species? About as good, I should say, as finding, while wandering through an uninhabited wilderness, an inn whose loosely closed door opened at a tap, and led to a table excellently spread, and a bed prepared for the weary traveler. It is easier to believe that the Cecropia has developed these three rare features not by chance—in the sense that they are unrelated—but rather through natural selection, because they are useful in making it an attractive home for the ants that protect it from its enemies. Such was Schimper's view. Let us see now how effective in guarding the tree the ants really are.



YOUNG CECROPIA SHOOT OPENED
REVEALING 11 INTERNODAL CHAMBERS, EACH ONE SURROUNDED BY THE WHITE REMNANTS OF CENTRAL PITH.

We may as well begin by considering the effectiveness of these Azteca ants in guarding their home tree against those creatures most destructive to vegetation—with shame I write it—man himself. As one of the abundant plants in the tall second-growth thickets, which in the Tropics are cut and burned to make fields for maize, rice, and other crops, the Cecropia is especially subject to attack by the long machete of the agricultural laborer. The garrison of ants serves not at all to protect the tree—and themselves—from destruction by his swinging blade; Cecropia trees are leveled indiscriminately with all the lush growth of giant herbs, bushes, vines, and other trees among which they form so conspicuous an element. The sweating laborer is indeed often bitten by the Azteca ants; but they are among the less formidable of the hosts of ants of many kinds and habitats whose bites and stings—along with those of a variety of other insects—are an inseparable accompaniment of his toil.

For the Aztecas can only *bite* with their mandibles. Their mode of attack is entirely mechanical; no venom is injected into the victim. Ants capable of inflicting really severe punishment *sting,* like honeybees, with the end of the abdomen, injecting a drop or so of formic acid. Neither biting ants nor biting bees—of which tropical America contains many kinds—command the same respect as their stinging relatives. I would rather endure the gnawings of a score of the Cecropia's ants than one fierce sting of the long, slender ants that dwell in the bull-horn acacia, or, for that matter, of one of the tiny brown fire ants so annoyingly abundant about houses and lawns in tropical America. The Aztecas, weak and not particularly agile, are seriously incommoded by hair no denser than that on the back of a man's wrist. A few of them biting away at the tough skin of a man's hands are of no great consequence. It is only on the tender skin of the neck and parts of the body habitually clothed that they cause much discomfort.

Cecropia trees are as a rule left unmolested by man, except when he is clearing land for sowing and other purposes, largely because they are of little use to him. Sometimes a segment is removed from a felled trunk, exposing the central hollow, which then serves as a gutter for conducting water—perhaps the only available substitute for a pipe in forest communities remote from both steel mills and native bamboos. The tough fiber in the bark is sometimes twisted into rope or used for making hammocks; but where the *burío* (*Heliocarpus*) or the *jucó* (*Trema*) are available, the Cecropia is rarely disturbed for this purpose. The choice is determined by the superior fiber of the first two, not by the ants in the last. Yet the botanist will admit that Cecropia trees are unpleasant plants to collect; if the ants are individually

THREE-TOED SLOTH (*BRADYPUS GRISEUS*)
IN PANAMA THIS ARBOREAL MAMMAL SOMETIMES COMPLETELY DENUDES CECROPIA TREES OF THEIR FOLIAGE.

not formidable, their very abundance is troublesome.

One has only to watch an Azteca ant struggling among the hairs of his forearm to suspect that on the body of a furry animal the insects would be as incapable of rapid and effective action as a man might be in the midst of the debris of a newly felled forest. Mammals of several kinds consume large quantities of the foliage of the Cecropia. The howling monkeys—those agile browsers of the tree tops—are fond of its great leaves and tender catkins; and in regions where they abound their vociferous bands are often seen among its branches. When first, in Panama, I studied Nature in the common range of the Cecropia and the howling monkey, I was reluctant to believe that the particular trees in which the monkeys foraged were indeed infested by ants. It seemed more likely—to one influenced by the writings of Schimper—that they had somehow escaped colonization by the Aztecas. I recall vividly how, years ago, I cut into the trunk of a tall Cecropia, whose growth in girth had quite obliterated the lower of the ants' perforations for ingress and egress, while the howlers that had been feasting among its lofty branches shouted down their protests. But when I reached the hollow center the little Aztecas swarmed out; and I knew then that they were ineffective in guarding the tree against the depredations of the monkeys. These animals, it is true, devote a very considerable portion of their time to scratching themselves; but the amount of this activity bears no relation to the kind of tree in which they happen to be; and doubtless it is their own parasites rather than the Azteca ants that cause them discomfort.

Another tree-top browser very fond of the foliage of the Cecropia is the three-toed sloth (*Bradypus griseus*). This phlegmatic creature, whose existence appears so nearly vegetative, seems to have definite tastes in foliage. In western Panama, the sloths appear to prefer the Cecropia to other trees; just as in the highlands of Costa Rica the two-toed sloth (*Choloetis hoffmanni*) is found eating the



leaves of a certain tree (*Brunellia costaricensis*) too often for it to be considered a mere matter of chance. Of five three-toed sloths that I saw in one day, while paddling along a lagoon in western Panama, four were in Cecropia trees. One of these, a female carrying her baby upon her breast, was descending the trunk of a Cecropia that had been defoliated to the last leaf. In eating, as in other activities, the sloth is quite as slow and deliberate as its name implies; a single large Cecropia leaf will engage its attention for half an hour or more; and a denuded tree indicates long and persistent activity by the beast. One might suppose that the Cecropia would produce leaves faster than a sloth could consume them. Like the monkeys, the sloth devotes a large share of its waking hours to scratching, with a steady, deliberate, mechanical action that scarcely reveals any trace of irritation or of feeling. But in this instance, too, the source of irritation appears to be other than the Azteca ants, which can scarcely find their way through the beast's coarse, dense pelage. When sated with its meal of foliage and finished with its scratching, the sluggish creature seeks the crotch of a stout limb, bends its head forward until its short, dull face is hidden between its forearms, and remains quietly sitting and slumbering upright in the fork, a featureless mass of gray hair, all oblivious of the ants that crawl over the limbs all around it.

Birds of many kinds visit the Cecropia tree, either to rest among its branches—where the ants appear never to molest them—or for more special purposes. The thick, green, fruiting catkins are a food attractive to fruit-eating birds as diverse as oropéndolas, toucans, barbets, cotingas, and finches, which help scatter the tiny seeds far and wide and are responsible for the far-flung distribution of the tree. In the upper Térraba Valley of Costa Rica, these catkins are probably the most important food of frugivorous birds during the early months of the year, when fruits of other sorts are scarce. Other birds, from big squirrel cuckoos to little wintering wood-warblers, seek the varied insects that thrive upon the succulent foliage. Although its coarse, open branch-system makes the Cecropia a poor site for nests, yet a few kinds of feathered creatures build their homes upon it and raise their families without molestation by the ants; just as birds of more numerous kinds place their nests in the bull-horn acacias, evidently taking advantage of the protection afforded by the fiercely stinging ants that dwell in the thorns. The bulky, domed nests of the chipsacheery flycatcher (*Myiozetetes similis*) are not infrequently built in a crotch of a Cecropia tree.

Most of the feathered visitants to the Cecropia tree are beneficial, either in scattering its seeds or in removing insect pests. The theory that the Azteca ants are present as a standing guard of the tree would not require that they keep these birds away. But one bird that habitually frequents the Cecropia, and certainly does it more harm than good, is attracted by the ants themselves. The big pileated woodpecker (*Ceophloeus lineatus*), a black bird with a flamboyant scarlet crest, pierces young trunks and the slender branches with its powerful chisel-bill, to extract the ants and their pupae from the hollow center, now and again pausing in its work of perforation and extraction to pluck off great numbers of the unfortunate Aztecas that swarm over the bark. In widely scattered portions of its range, I have times without number watched this myrmecophagous woodpecker at its feast. These ants are an important constituent of the bird's diet. Like those other ant-eating members of the family, the flickers, the pileated woodpecker feeds its nestlings by regurgitation. This mode of bringing food to the nest is less prevalent among the New World woodpeckers than that of carrying it in the bill and has perhaps been developed in relation to the smallness of size of the individual particles that form the diet of those kinds subsisting largely upon ants. The holes made in the branches and young trunks of the Cecropia are closed at length by wound tissues that eventually form great tumorous protuberances; but many young trees break across at the point where they have been pierced low in the stem. Trees that have received much attention from the woodpeckers are less flourishing than their undisturbed neighbors, while their ant colonies are greatly depopulated. In regions

AN OROPÉNDOLA

THIS BIG COUSIN OF THE ORIOLES EATS THE FRUITING CATKIN OF CECROPIA. THIS IS A YOUNG BIRD.

where the woodpecker is abundant, it is incredible that the ants can be of sufficient service to the tree to compensate for the tremendous injury that their presence brings upon it.

To the pileated woodpecker the Cecropia is alluring in proportion to the number of ants it shelters; but to a number of small birds of quite different tastes it is most attractive when the Aztecas are few or absent. For only in the absence of the ants do the little white protein corpuscles become abundant and prominent on the furry cushions at the bases of the petioles; and when this occurs they offer a dainty food to a variety of small birds. I have watched twelve species take advantage of this food. The little, yellow-breasted Mexican honeycreeper (*Coereba mexicana*) is fond of these tidbits, which may form a not unimportant article in its diet. In parts of its vast range as distant as Costa Rica and Ecuador I have repeatedly seen the tiny bird pluck off the minute white bodies with the sharp tip of its strongly curved black bill. The Parula warbler of the Tropics (*Compsothlypis pitiayumi*) feasts upon these dainties; while such wintering members of the family as the Wilson warbler (*Wilsonia pusilla*), the Tennessee warbler (*Vermivora peregrina*), and even the thicket-haunting mourning warbler (*Oporornis philadelphia*) have also discovered their secret. Among finches, the Mexican grassquit (*Tiaris olivacea*) and the seedeaters (*Sporophila* spp.) sometimes eat them; among tanagers, the euphonias (*Tanagra* spp.) and the blue-rumped tanager (*Calospiza gyroloides*); while in the highlands of Costa Rica the queer little ovenbird known as Lawrence's spinetail (*Acrorchilus erythrops*) consumes them in numbers. In this same region dwells the biggest bird that I have seen eat the protein bodies, the yellow-thighed sparrow (*Pselliophorus tibialis*), which is a finch as large as the towhee. In the excessively wet mountains where the spinetail and this sparrow dwell, the hollow stems of the Cecropia are much of the time flooded with water, with the result that they contain no ants to share the protein bodies with the birds. The visits of all these small birds are of no importance to the tree, nor do they help us to decide whether the Azteca ants form an effective guard; yet their presence is further evidence of the multiform bounty of the Cecropia.

But it is was not in defending their home tree against birds and four-footed animals, so much as against the depredations of other insects, that Schimper supposed the garrison of Azteca ants to be of greatest service. Yet frequently one sees a Cecropia with its foliage more or less damaged by leaf-eating insects. Sometimes the softer tissues of the great leaves are all but consumed by a budworm, even on trees with a thriving colony of ants. My own observations, made largely north of the Equator, are in full accord with those of Karl Fiebrig, who years ago, from studies made in Paraguay near the southern limit of the Cecropia's vast range, concluded that the ants were ineffectual in protecting the trees from a variety of insects and their larvae.

But in the Tropics perhaps no insects as a class are more injurious to vegetation than ants themselves. Abundant as these creatures are in the Temperate Zones, no one who has not actually lived in the tropical lowlands can form an adequate conception of their numbers and variety in regions of perpetual warmth. From crevices in the soil and the rocks to the topmost branches of the



great forest trees, they swarm everywhere in unbelievable variety and abundance. At times one's dwelling will be invaded by a horde of Echiton, or army ants, which flow like a stream through every nook and cranny, seeking out the small creatures of every kind on which they prey. These carnivorous legions perform their generally beneficial work of clearing the house of vermin and pass on; but smaller ants of various kinds are always present; and no food escapes their depredations unless stored in a sealed container or in a cabinet with legs set in water. The nests of these tropical ants are of the most astounding variety. Some are placed in the ground; some hang like great gray stalactites from the lofty boughs of trees; some occupy hollow dead branches; others are woven of finest silk secreted by the larval ants, among living foliage skillfully attached to the walls. It is not surprising that the hollow living organs of many species of plants should have been discovered and occupied by ants, which during the course of ages became specially adapted to life in these snug retreats, and in turn gradually produced changes in the structure of the host, thereby developing the curious phenomenon of myrmecophily.

The agriculturist in the Tropics wages a never-ceasing war against the battalions of the ants. They devour his seeds if germination is slow; they bite the young and tender tissues of plants, enlarge crevices in the bark of fruit trees for their nests, damage young sprouts by covering them with earth, spread mealy aphids over his sugarcane. Since turning attention to practical agriculture in the Tropics, I find it increasingly difficult to hold faith in Schimper's view that the extrafloral nectaries so common in the plants of warm regions are of service by attracting beneficial species of ants. I have never known a husbandman in tropical America who had a good word for the ants. Yet in the Orient the situation may be different. In Java the natives of certain districts collect, in the forest and among the trees along the seacoast, nests of a kind of large and fierce red ant, which they hang in their mango trees. Here the ants protect the developing fruits by devouring the larvae of a beetle (*Cryptorrhynchus mangifera*) capable of causing great damage. The Javanese are said to attend these red ants with care, providing flesh to suit their carnivorous tastes, destroying other kinds of ants that are hostile to them, and joining the mango trees together by bridges of bamboo to facilitate the insects' visits to all parts of the grove. In ancient times the Chinese orchardists collected and propagated ants, which they placed in their orange and tangarine trees to keep them free of caterpillars. There was actually a special class of laborers who collected the ants.

But these husbandmen of the Far East never had to contend with the leaf-cutting Attas, which of all ants in tropical America do most conspicuous injury to vegetation. The nest of these brown spiny ants is made underground, and with time it becomes a far-flung labyrinth of chambers and intercommunicating tunnels, beneath the wide bare mound of earth thrown out during the course of their excavation. From the mound as a center, narrow, well-defined pathways, kept clean and bare of vegetation by the ants, extend far and wide over the neighboring terrain. Along these myrmecine highways a stream of ants is constantly flowing: huge-jawed, deliberately stalking soldiers, slender workers of medium size hurrying to their tasks, and tiny ants whose function is not at once apparent. Those traveling outward from the nest go unburdened; but in the returning stream a large proportion of the workers bear in their jaws pieces of green leaf far larger than themselves, rising above their backs like irregular standards or sunshades. Hence comes the name, parasol ants, sometimes applied to them.

Each bit of leaf is cut by the scissorlike mandibles of a worker ant from the foliage of a growing plant, whether tree, shrub, or herb. As it is borne along by the worker toward the nest, another smaller ant, or sometimes two or three together, may be seen clinging to the already huge burden and being carried toward the mound. Doubtless these riders are attempting to bear the burden themselves; but the strongest of those attached to the bit of leaf lifts the would-be helpers into the air and marches off with both cargo and assistants. Arrived at the nest, the pieces of leaf are carried into the

subterranean chambers and cut by the jaws of the ants into fine bits, which form a sort of compost heap, upon which a special kind of fungus is grown. The ants eat, not the leaf, but the fungus, which produces a profusion of minute, knoblike bodies in white, flocculent masses. It is supposed that the duty of the smallest class of workers is to weed the fungus gardens, removing all kinds of fungus growths except that upon which the population subsists. When they have served their purpose, the discolored bits of leaf, far from being eaten, are thrown out upon midden heaps near the entrances to the burrows.

Though these ants make use of the foliage of a great variety of plants native to tropical America—indeed, these were the only kinds available to them during the long centuries before Europeans, following Columbus, brought the products of the Old World to the New—some writers have thought they detected a special fondness for the leaves of cultivated species introduced from the Eastern Hemisphere. This seeming preference may be caused by the circumstance that in plantations, where little variety is within their reach, the Attas make severe attacks upon the dominant plant. A colony established in a lawn may almost defoliate the nearest ornamentals, whereas in the forest, with so many plants of so many kinds available, they show slight preference for particular species, and their injury to the vegetation is less evident. But it is certain that in many districts one cannot profitably grow his crops, or enjoy beautiful shrubbery and flowers about his dwelling, without waging unremitting warfare against the leaf-cutters. Great coffee plantations employ squads of men for the sole purpose of destroying their nests, either by pumping poisonous gases into them or by digging them out, leaving great holes large enough to bury a yoke of oxen. The farmer may feel a bond of sympathy with these fellow agriculturists even as he proceeds to destroy them; but he knows very well that he and they cannot both make a living from the same farm.

Are the Azteca ants of the Cecropia tree an efficient guard against the destructive leaf-cutting Attas? Schimper believed that they are. Examine a hundred Cecropias, even in a district where leaf-cutting ants abound, and few if any will show severe injury by them. But the same would be true of almost any other kind of tree, native or introduced, except in plantations and dooryards where the bare soil invites the establishment of Atta colonies, and they have little variety of vegetation to choose from. Rarely the Atta ants make great inroads upon the foliage of a Cecropia, cutting away the great leaves until only the principal veins remain, each margined by a narrow strip of tissue with circular indentations that reveal the ants' mode of work. I have seen such depredations on Cecropias that supported a flourishing colony of Aztecas.

For several months I have been looking for a Cecropia that gave evidence of the work of the Attas, but without success. This might be construed to favor the theory of mutual protection; but I have also failed to see the leaf-cutting ants at work upon a *burío* (*Heliocarpus*), a soft-wooded, swift-growing tree of the same habitat as the Cecropia and no less abundant, but with solid stems that provide no accommodation for ants. The Attas are happily not very abundant in this district—except in our canefield.

Finally, in order to witness what would happen when Atta and Azteca came face to face, I captured a few leaf-cutting ants and placed them upon the stem of a young Cecropia tree. The occupants were mostly indoors; and the unintentional trespassers wandered aimlessly about without meeting them; so I shook the sapling to bring the Aztecas outside. The little ants came pouring out their narrow doorways and raced about over stem and leaves, as if seeking the cause of the disturbance. Many of them passed close by the Attas; and often they ran beneath the longer-legged brown ants, without paying any attention to them. This might happen a number of times, and the interlopers remain for several minutes unchallenged in the midst of the swarming Aztecas. But sooner or later an Azteca would seize an Atta by a leg, or more rarely the body, and then one of several things might happen. Sometimes, in a manner difficult to understand, the tiny Azteca would throw the big Atta from the tree, retaining its own hold. Far oftener the tussle would continue until the unequal adversaries fell, clutched together, to the ground. Or, if the struggle was long-drawn-out, other Aztecas, bumping into the contestants, would join the fray. Although many of the smaller ants might brush against an undisturbed Atta and pass on, every one that came within touching distance of an ant already attacked would at once seize upon it. Soon the unfortunate leaf-cutter would be in the midst of half a dozen angry little Aztecas, pulling out its long legs this way and that, biting its hard brown body, until at length the whole writhing mass fell from the tree. Some of the Attas, especially the larger workers, easily repelled each attacking Azteca with a single nip of their powerful mandibles and went wandering around until they reached the ground.

The same was true of some large black ants with golden abdomens that I found on the Cecropia trees—the Aztecas were helpless against their strong jaws. There is no doubt that the Cecropia tree's garrison of ants attempts to repulse invading ants, in many instances with success. But if they are not stirred up, as in my experiments, a foreign ant might wander far over the tree without meeting a defender; and the latter often proves entirely neutral when at last contact is made. The Attas placed one by one upon the Cecropia were lost, aimless, far outnumbered. From what I saw it was not difficult to picture a whole organized column of them mounting the trunk of an otherwise undisturbed Cecropia and cutting the leaves, without meeting real resistance from the supposed garrison. But resistance or no resistance, they are quite capable of carrying off the foliage of a well-populated tree when they want it.

Monkeys, sloths, woodpeckers, honeycreepers, and many other birds, Azteca ants, leaf-eating insects, and at times even Atta ants—are they not all in the same category, guests that come to partake of the bounty spread for them by the most hospitable tree of the Tropics? Some do it harm by stripping it of foliage or drilling holes in its trunk; others, as the small birds that eat the protein bodies, and apparently also the Azteca ants themselves, appear neither beneficial nor directly harmful; only the larger fruit-eating birds that scatter its seeds far and wide, and the insectivorous species that remove caterpillars from the leaves, are an undoubted positive benefit. The Aztecas, instead of a formidable guard to repel all intruders from an inhospitable tree, may be simply the foremost beneficiaries of a bountiful one.

But the admission that the most distinctive is also the most hospitable tree of tropical America forces us to concede it still a third superlative. For to deny that the ants are of positive benefit to the tree is to refute the only plausible explanation that has been advanced for the evolution of its three great structural peculiarities: the exceptionally wide central hollow of the stem, the furry protruding leaf bases with their protein bodies, and the pits that facilitate the perforation of the wall surrounding the hollow internode. Without some single use to which all three contribute, how can we account for the presence in a single species of features that would be surprising enough as random developments in three different families? The mystery still challenges us. The Cecropia is the most enigmatic tree of tropical America.