

IV.—ANTS IN THEIR DIVERSE RELATIONS TO THE PLANT WORLD

By J. BEQUAERT

The following contribution is an attempt to summarize what is known at present of the widely varied and often intricate relations which exist in nature between ants and vegetation. It has primarily grown out of an examination of certain so-called "myrmecophytes," or ant-plants, which I frequently came across during my travels in the Belgian Congo in quest of zoological and botanical specimens. Prof. Wheeler's study of the feeding habits of the larvæ of certain plant-inhabiting ants collected by Messrs. H. Lang and J. P. Chapin and myself in the Congo, and Prof. I. W. Bailey's investigation of the anatomy of myrmecophytes show that the whole subject of the mutual adaptations of plants and ants is in need of a thorough revision. It thus seemed appropriate that the present opportunity be used to bring together the many isolated and scattered observations which have been made on the interrelations of these organisms. Indeed, the problem of myrmecophytism is dominated by the feeding habits of the ants and their young and, until these are perfectly understood, we can scarcely hope to grasp the true ecological meaning and the probable origin of the extreme cases of apparent or true symbiosis between certain ants and certain species of plants. It is, therefore, of the utmost importance to inquire carefully into the various ways in which ants are wont to benefit by the vegetation.

Although much time has been spent in consulting botanical and entomological papers for information bearing on the subject, undoubtedly a number of interesting observations have escaped my notice. In keeping with the general purpose of the present contribution to African Myrmecology, especial attention has been paid to work accomplished in the tropics, primarily in Africa. The bibliography appended to this part is as complete as possible. In it are included many papers which may seem to have but remote connection with the subject—such as, for instance, those on fungus-growing termites, intracellular symbionts, and the like. I believe, however, that they are indispensable in reference to the study of certain activities of ants. Some students may find the botanical side rather too fully treated, but this seemed unavoidable in providing the necessary background for future field work, especially to the myrmecologist. Moreover, I am convinced that the ultimate solution of many of the problems involved can only come from a close cooperation between botanical and entomological experts, and this, under present conditions of specialized training, is not so easily realized.

Many of the data here presented were brought together during the several weeks I had the pleasure of spending at the Bussey Institution for Applied Biology of Harvard University. I wish to thank President Henry Fairfield Osborn and the authorities of The American Museum of Natural History for the liberal manner in which I have been able to carry on this work. I am also under great obligations to Professors Wm. M. Wheeler and I. W. Bailey, of Harvard University, for their many suggestions and criticisms during my stay at the Bussey Institution. The interest they have shown in the work has been a steady encouragement and their advice invaluable.

1. VARIOUS RELATIONS BETWEEN ANTS AND VEGETATION

Economic Importance of Ants

The question whether ants are, broadly speaking, noxious or beneficial insects is still debated by agriculturists and economic entomologists.

While it is believed on the one hand that ants attack and mine only sick and decaying plants, especially decaying roots, on the other hand it is claimed that healthy plants, which show no trace of disease, are also assailed by ants. In any case further exact observations concerning the relation of ants with plants will be needed in order to clear up this problem. The elucidation of the question of the direct noxiousness of ants to plants is the more desirable, since we possess in the ants partly a welcome help against other animal enemies of culture-plants, which they pursue and destroy. It is therefore necessary that we learn more in detail whether their harmfulness outweighs their utility or vice versa. In general one can perhaps say that, judging from statements which have been made thus far, their noxiousness to plants, by attacking roots, stems or branches, is not very great. (G. Aulmann and W. La Baume, 1912, p. 61.)

In their recent study on the feeding habits of ants, Wheeler and Bailey (1920, p. 236) have pointed out that one reason why the economic importance of many common ants remains so dubious or ambiguous is the lack of precise information with regard to the quality and quantity of their food, especially in the larval stage. These authors have shown, for instance, that ants carry on their bodies and in the food-pellets of their infrabuccal pockets an extraordinary number and variety of fungus spores and bacteria. It is, therefore, quite possible that these insects have a great but hitherto only vaguely apprehended importance as carriers of the germs of certain plant, animal and human diseases. That ants are active carriers of pathogenic micro-organisms has been further suggested by Darling (1913), Wheeler (1914), Studhalter and Ruggles (1915), Grabham (1918), and Bailey (1920).

The leaf-cutting ants of the tribe Attini, so abundant in tropical and subtropical America, are decidedly destructive to the vegetation and are rightly considered one of the worst pests to South American agriculture. Accounts of their depredations are found in practically all narratives of South American travellers. Though they attack many of the native herbs, shrubs, and trees, they often show a predilection for cultivated plants. It is no uncommon thing to find the sauvas, *Atta cephalotes* (Linnaeus), so numerous in certain spots that the planters are forced to abandon their fields. Speaking of the ants in the Brazilian coffee districts, Van Delden (1885, pp. 297-298) writes: "The enemy most dreaded in the fazendas (plantations) is indubitably the saúva, or tana-jura, a dark-brown ant, two centimeters long, which undermines the ground by digging extensive passages and dens in all directions. It attacks all sorts of trees, the coffee-shrub among others, but has a decided preference for the orange and citron trees in the coffee gardens." H. W. Bates (1863) and others have noted that these ants often become troublesome to the inhabitants because of their habit of plundering the stores of provisions in houses at night.

The Attini are not represented in the Old World tropics, but possibly ants of other groups have developed similar habits there, though on a smaller scale. G. Aulmann (1912, p. 156) and Moorstatt (1914) mention that a leaf-cutting ant was observed in German East Africa at times causing considerable damage to cotton plants. The specific identity of this ant has not been ascertained, but it probably belonged to the genus *Messor*, which is known to collect pieces of grass in addition to seeds and grain (see Sjostedt's observation quoted below, p. 359). King (1911) also notes that *Messor barbarus* (Linnaeus), at Khartum, damages garden plants by biting off and carrying away the leaves, and adds that in cotton fields the sites of their nests are marked by bare patches devoid of vegetation. What use these ants make of the vegetable matter thus carried into their nests has not been investigated.

There are a few other cases on record of ants directly destroying living parts of plants. It is generally known that certain ants will injure buds and fruit in order to feed on the exuding sap (see Muller-Thurgau, 1892, pp. 131-135). Forel (1885, p. 338) mentions instances of *Tetramorium caespitum* (Linnaeus) attacking young roots of healthy sugarbeets at Vaux, Switzerland, many of the plants dying from the injuries received. J. Pérez (1906, pp. xxxii-xxxiv) records the havoc played by the same ant on the tubers of potato, near Bordeaux, more or less deep cavities being excavated and many young plants killed; *T. caespitum*

was also found burrowing superficial galleries in the stems of living potato plants and attacking the roots of young cabbage and carrot.¹ In North America, *Solenopsis geminata* (Fabricius) and *S. molesta* (Say) often do injury to the soft parts of planted seeds, and the former also to strawberries (Webster, 1890) and other fruit. *S. molesta* has proved very injurious in gardens and fields; the chief damage is done to seeds of sorghum and corn, which are hollowed out undoubtedly for the purpose of extracting the oils (McColloch and Hayes, 1916; Hayes, 1920). According to Green (1900a) and G. R. Dutt (1912, p. 247), the Indian *Dorylus orientalis* Westwood is mainly or exclusively herbivorous, feeding on the bark of trees and the healthy tubers of plants, a habit the more remarkable since the majority of Dorylinae are highly carnivorous. In Cameroon, certain ants have been seen attacking the fruits of cacao-trees: *Camponotus maculatus* subspecies *brutus* (Forel) gnaws the base of fruit-stalks where they are inserted into the trunk, licking up the sap at the wound, causing the fruits to drop off or dry; *Crematogaster africana* variety *winkleri* (Forel) gnaws away the skin of the cacao-fruit, often almost completely; while *Camponotus acrapimensis* Mayr and *Ecophylla longinoda* (Latreille) are accused of the same evil, though they cause but little damage (H. Winkler, 1905, pp. 129-137).

The greatest harm to the vegetation is undoubtedly done indirectly, both in tropical and temperate regions, by a host of species of ants that have a pronounced fondness for pasturing and guarding plant lice, scale insects, tree-hoppers, and other plant bugs on roots, stems, and foliage; all these Hemiptera suck the juices of plants, and their protection by the ants must, therefore, be regarded as pernicious. The "milking" habit among ants seems to be of very frequent occurrence, evidently because it offers so many advantages over direct feeding on plant-juices. Not only is the food supply much more abundant at any one time and within easier reach, but, in addition, the plant saps undergo chemical changes in the digestive tract of the Hemiptera, whose anal secretion, on which the ants feed, therefore contains a great amount of invert-sugar, instead of the much diluted cane-sugar of the plant. Many of the aphids attended by ants have undergone adaptive modifications of structure and behavior which show that their relations with ants have become of a mutualistic nature, and it is probable that the same will be found true for some of the ant-attended coccids and membracids of the tropics.

¹This habit of *Tetramorium caespitum* in attacking subterranean parts of plants was known to Linnaeus, since he adds to the original description of this ant (*Syst. Nat.*, Ed. 10, 1, 1758, p. 581): "Habitat in Europa tuberibus." It is rather surprising that injuries by this ant have been so little noticed in later times. Concerning ants noxious in gardens, see also F. Heim (1894), Andersson (1901), and Cooley (1903).

Indeed, the association between phytophagous Hemiptera and ants offers a typical illustration of symbiosis in the strict sense, advantageous to both parties. The benefit that accrues to the ants has been explained above and needs no further comment; that derived by the Hemiptera, however, is of a more complex nature. It is obvious that the ants protect the plant bugs by driving away coccinellid beetles, ichneumon flies, and other enemies. In the case of aphids and coccids the ants frequently build tents or cowsheds over these insects, which thus continue to suck the juices of the plant while being "milked" by the ants and are, at the same time, protected from their enemies, from alien ants, and intemperies, and prevented from escaping to other plants.

The tent-building habit was discovered by P. Huber (1810, pp. 198-201) for *Lasius niger* (Linnæus) in Europe, and Forel (1874, pp. 204-205 and 420-422) gives an interesting account of it in his classical 'Ants of Switzerland.' *Lasius niger* has similar habits in North America (Wheeler, 1911b) and Japan (Stopes and Hewitt, 1909, pp. 1-6). This ant builds its tents of detritus or wood-fibres; while, according to Forel, certain species of *Myrmica* enclose their aphids in earthen cells, which communicate with the ground nest by means of covered galleries. Wheeler (*loc. cit.*) has described in detail the tent-building of the North American *Crematogaster lineolata* (Say) and I have found that several African members of this genus which attend coccids have similar habits. Certain North American species of *Lasius* (*L. flavus*, *L. niger*, and the species of the subgenus *Acanthomyops*) which live to a very large extent or exclusively on the excrement of root-aphids and coccids, remain throughout the year the constant companions of the lice, even hoarding in their nests during winter the eggs or the wingless, agamic form of the aphids and the fertile females of the scale insects. Forbes (1896), Webster (1907), and others have shown that the common North American *Lasius niger* variety *americanus* Emery guards the eggs of the corn root aphid (*Aphis maidi-radicis* Forbes) throughout the winter, shifting them about, as it does its own young, to accommodate them to changes of weather and moisture. In spring, the young lice, on hatching from these eggs, are conveyed by the ants during fair weather to the roots of various weeds, being taken back to the burrows in bad weather or on cold nights. After the corn plants have started to grow, the young root lice, all of which belong to the wingless, agamic form, are transferred from the weeds to the roots of young corn, where they are tended throughout the spring and summer. It would thus appear that, without the aid of the little brown ant, this aphid is unable to reach the corn plants.

Still more surprising is Lubbock's observation that *Lasius flavus* cares in a similar manner for the eggs of certain aphids on the aerial portions of plants.

The eggs are laid early in October on the food-plant of the insect. They are of no direct use to the ants, yet they are not left where they are laid, where they would be exposed to the severity of the weather and to innumerable dangers, but brought into their nests by the ants, and tended by them with the utmost care through the long winter months until the following March, when the young ones are brought out and again placed on the young shoots of the daisy. This seems to me a most remarkable ease of prudence. Our ants may not perhaps lay up food for the winter, but they do more, for they keep during six months the eggs which will enable them to procure food during the following summer. (Lubbock, 1880, p. 184.)

In temperate regions the honeydew (or sugary excrement) secreted by aphids from the posterior end of the alimentary canal is eagerly sought for by many of the common Myrmicinae, Dolichoderinae, and Formicinae,¹ those attending root lice being especially harmful to the vegetation for the reasons mentioned above.² Certain tropical ants also nurse root-aphids. In Java, *Acropyga acutiventris* Roger may thus become a serious pest to coffee plantations, and, according to Forel, various species of *Rhizomyrma* attend root lice in South America and New Guinea (K. Eiseherich, 1911b, p. 227, foot note). In the tropics, however, aphids are far less common than in colder climes and are there replaced as ant "cows" by various Coccidae, Membracidae, Fulgoridae, Cicadellidae (Jassidae), and Psyllidae, certain members of these families being occasionally attended by ants even in North America and Europe.

The relations between various species of tree-hoppers and certain ants have been recently reviewed by Funkhouser in his 'Biology of the Membracidae of the Cayuga Lake Basin' (1917, pp. 399-404), to which the student is referred for further details. Funkhouser comments on the number of unsolved problems in connection with this subject.

One of the first of these questions is suggested by the fact that some of the species are attended by ants while others are unattended although there are apparently no physiological or anatomical differences to cause the distinction. Another question arises from the fact that certain species attended locally have never been reported as being attended in other parts of the country, while on the other hand some of the species that are never attended in this basin are always attended in other localities. Again, certain species that the ants ignore in this basin are represented by closely related species in other regions and these exotic forms—often of the same genus and very near systematically—are well attended.

¹It would appear that these trophobiotic habits are of great antiquity among ants, dating as far back as the Tertiary. Wheeler (1914, p. 21) found a block of Baltic amber containing a number of workers of *Iridomyrma opperli* (Mayr) together with a lot of their aphid wards.

²See the publications of S. A. Forbes on the corn root aphid, listed in the bibliography; also Garman's (1895) account of the bean root louse.

He also notes that certain common species which, in the nymphs at least, appear to exude the characteristic anal fluid when disturbed, nevertheless are not attractive to ants. He found the following species of Membracidae attended by ants in the vicinity of Ithaca, New York: *Thelia bimaculata* (Fabricius), *Telamona ampelopsidis* (Harris), *T. unicolor* Fitch, *Cyrtolobus rau* (Say), *Alymnus castaneæ* (Fitch), *Ophiderma pubescens* (Emmons), *Vanduzeca arquata* (Say), *Entylia bactriana* Germar, and *Publilia concava* (Say).

The following ants were actually observed by Funkhouser taking the secretion from the membracids: *Formica truncicola* subspecies *obscuriventris* (Mayr), *Formica exsectoides* Forel, *Camponotus pennsylvanicus* (DeGeer), *Crematogaster lineolata* (Say), and *Prenolepis imparis* (Say). All these ants seemed to make no distinction between the various species of tree-hoppers listed above and the mutual behavior of these insects was much the same in all the cases studied: "The ants stroke their charges with their antennæ, whereupon the membracids give off from the anal tube a liquid that issues in bubbles in considerable quantity. The anal tube of the membracid is capable of great evagination especially in the nymphs, in which it is long and cylindrical and usually tipped with a fringe of fine hairs. The honeydew is eagerly taken from the end of this tube by the ants. In many species the adults as well as the nymphs are sought, and the ants seem to be as attentive to one as to the other but the adults have not been observed to excrete the liquid to the same extent as the nymphs." (Funkhouser, 1917, p. 403.) The liquid sought by the ants "is colorless and transparent, rather heavy and somewhat sticky. When first exuded it is inclined to be frothy, due no doubt to bubbles of air which emerge with it, but it quickly clears on settling. It is practically tasteless even in comparatively large quantities, and many attempts to distinguish a sweet taste have proved unsuccessful. The term *honeydew*, therefore, commonly applied to the fluid, is hardly a descriptive one. It is very likely, of course, that the liquid may contain sugars not detected by the human tongue, and this would seem to be indicated by the fact that fermentation appears to begin if the substance is left exposed. No chemical analysis of honeydew has been made." (*Op. cit.*, p. 404.)

Miss Branch (1913, pp. 81-85) states that young *Entylia sinuata* seemed unable to molt successfully without the presence of ants. This fact led her to believe that the ants are necessary factors in the life of an individual membracid. Funkhouser's experiments, however, gave no support to this theory. Tree-hoppers of many species were reared

in the field and in the insectary, with and without ants, and no difference was noted in the length of the instars or success of the molting process.

Kornhauser (1919, p. 546) gives the following account of the manner in which *Thelia bimaculata* (Fabricius) is attended by ants. This membracid feeds on the sap of the common North American locust tree, *Robinia Pseudo-acacia* Linnæus. It deposits its eggs in slits in the bark, where they remain during the winter, hatching in early June. The first, second, and third instars occur on the branches, constantly attended by ants:

In my principal collecting fields [at Cold Spring Harbor, New York], *Formica truncicola* Nylander subspecies *obscuriventris* and *Cremastogaster lineolata* Say were the chief ants associated with *Thelia*. When tapped by the antennæ of the ants, the *Thelia* nymph or adult exudes from the anal tube a drop of clear fluid which is taken by the ant with great alacrity. Toward the middle of June, the ants build collars about the bases of the locust trees, and inside these collars in the cracks of the bark are to be found hundreds of *Thelia* nymphs of third to fifth instar, quietly feeding and undisturbed by the numerous ants in attendance. In this moist situation, protected from many of their enemies, the nymphs thrive. *Formica* builds the protecting collar of leaves, twigs, and bits of wood; *Cremastogaster* builds of sand grains cemented together. When one breaks the collar, many ants swarm out and attack the intruder, *Formica* biting one's fingers ferociously, while others grab the *Thelias* and drag them into underground passages. These pugnacious ants seem to have complete mastery of the *Thelia* nymphs.

Membracidæ are sometimes carried by ants into their formicaries (Enslin, 1911, pp. 19-21; W. M. Mann, 1915, p. 162), but they usually die soon, probably due to lack of food.¹

Lamborn (1914) has described in detail several cases of trophobiosis between ants and coccids, membracid, jassids, and psyllids in Southern Nigeria. Regarding *Leptocentrus altifrons* Walker, a tree-hopper which is invariably ant-attended in its mature and larval stages, he writes as follows: "The solicitude of ants for the larvæ has a very definite object, for they are extremely partial to the fluid excreted at the anal extremity, and I remember seeing a *Camponotus akwapimensis* variety *poultoni* with the caudal whip of a membracid larva actually in its mouth." (Lamborn, 1914, p. 495.) I have on several occasions, in the Belgian Congo, collected ants which were in the act of attending tree-hoppers: so, for instance, in April 1912, at Elisabethville, Katanga, a number of workers of the common *Pheidole megacephala* subspecies *punctulata* (Mayr) were

¹Additional information concerning the relations between Membracidæ and ants is given by Belt (1874), Mrs. Rice (1893), Green (1900c), Froggatt (1902, p. 717), Baer (1903), Buckton (1903, p. 262), Poulton (in Buckton, 1903), Distant (1908, p. 209), Enslin (1911), Miss Branch (1913), Kershaw (1913), Lamborn (1914), and others.

busily engaged in licking the sweet excretions of some of these hemipterous insects feeding on a bush; again, at Welgelegen, Katanga, *Myrmecaria eumenoides* subspecies *opaciventris* variety *congolensis* (Forel) was found attending membracids fixed on the calyx of a malvaceous plant (Bequaert, 1913, pp. 427 and 428). Bell-Marley at Durban, Natal, observed that the common South African tree-hopper, *Oxyrhachis tarandus* (Fabricius), attracts great numbers of "small red ants." (Distant, 1908, p. 209.)

The nursing of scale insects by ants has repeatedly been noticed by Cockerell, Newstead, King, and others.¹ A rather interesting phase is offered in the case of various ants which keep coccids inside the swellings of myrmecophytes. Zimmermann found *Lecanium tenebriophilum* Green at Buitenzorg, Java, together with ants in living branches of *Erythrina lithosperma* Blume (Green, 1904, p. 204). In southern Europe, *Crematogaster scutellaris* (Olivier) and *Camponotus pubescens* (Mayr) often become harmful to olive trees by the care they bestow upon scale insects (Peragallo, 1882). Keuchenius (1914a and b) holds the view that *Ecophylla smaragdina* is very noxious to coffee plantations through its habit of keeping and protecting in its nests the green coffee scale, *Lecanium viride*, one of the most serious pests to the coffee tree. Gowdey (1917) also mentions that the root form of *Pseudococcus citri*, a parasite of coffee, orange, lemon, and cacao in Uganda, is attended by the ant *Pseudolasius gowdeyi* Wheeler.

Most of the wood-boring ants either accommodate themselves to pre-existent galleries made by other insects or attack dead wood only. Occasionally they find their way into houses. Forel (1874) and R. Brun (1913) have described cases in which populous colonies of the European *Camponotus ligniperdus* and *C. herculeanus* had excavated the beams, window-sills, and other wooden parts of buildings. Certain carpenter ants of temperate regions (*Camponotus ligniperdus*, *C. herculeanus*, *C. pubescens*, and others) extend their burrows into healthy wood (Forel, 1874); they may thus become very destructive in forests, the more so since they attract woodpeckers, which bore large access-holes through the perfectly healthy outside layers of the tree in order to feed on the carpenter ants and their brood. S. A. Graham (1918) describes how carpenter ants of an unidentified species are responsible for great damage to stand-

1. The following authors (1874 and 1882) have mentioned the fact that ants attend to scale insects: Cockerell, Newstead, King, and others. In their respective works, they have also mentioned the fact that ants attend to scale insects on the stems of the olive tree, the orange tree, and the lemon tree. The following authors (1882) have also mentioned the fact that ants attend to scale insects on the stems of the olive tree, the orange tree, and the lemon tree: Peragallo, Keuchenius, and Zimmermann.

ing white cedar in Minnesota, at least twenty per cent of the trees cut showing ant injury to the stump. In this case, so far as observed, the ant never attacks a sound tree, but always gains entrance through a wound or decayed spot. When a colony has been established in a tree, the ants usually work well above the rotten area into the sound heart-wood, honey-combing the tree with longitudinal galleries until there is often only a thin outer shell of solid wood. From the main nest they cut openings to the outside, frequently following a knot, through which the sawdust can be cast and through which the inhabitants may pass to and fro. Ants which make their galleries in the bark (such as many species of *Leptothorax*) usually do not burrow beyond the external dead layers and occasion little or no damage, except in cases where the bark itself is of economic value: *Camponotus herculeanus vagus* (Scopoli) and *Crematogaster scutellaris* (Olivier) are credited with destroying the bark of cork-oaks in southern Europe and North Africa (Maccira, 1904; Emery, 1908; Seurat, 1901; A. Krausse, 1913 and 1919).

Harvesting ants have often been accused of depredations in cereal fields, but these charges are apparently much exaggerated. Emery (1891, pp. 176-177), it is true, has observed in Italy that species of *Messor* actively engage in carrying off grain during the harvest. It does not seem, however, that the damage thus done could be very serious, since harvester ants collect mainly seeds of weeds and wild grasses. Yet in certain regions of North Africa, where colonies of *Messor* are very numerous, the grain these ants store away may amount to an appreciable portion of the harvest. Ducellier (1912) estimates that, in Algeria, *Messor barbarus* collects 50 to 100 liters of wheat from each hectare. J. Pérez (1903, pp. xxxiv-xxxv) has recorded cases in which *Messor barbarus* stole freshly sown carrot-seeds and also the ripe seeds of coriander in a vegetable garden near Bordeaux. Similarly, Koningsberger (1908, p. 99), in Java, blames *Plagiolepis longipes* (Jerdon) with stealing planted seeds of tobacco.

A few species of ants are commonly found in houses, boats, and ships; they are spread by commerce to considerable distances, and rapidly become cosmopolitan.¹ Such domestic species in the Belgian Congo include, among others, *Monomorium pharaonis* (Linnaeus), *Tetramorium simillimum* (F. Smith), and especially the many forms of *Pheidole megacephala* (Fabricius); the last-named is the famous house ant of Madeira (O. Heer, 1852 and 1856), which has now established it-

¹Donisthorpe (1915, pp. 334-350) has given an interesting account of the exotic ants which have been introduced into Britain. His list includes fifty-one species, but only a small number of these have established themselves there; they are most commonly found in hothouses.

self everywhere in the tropics and subtropics.¹ In the Congo, the large workers of a form of *Camponotus maculatus* can also frequently be seen at night in houses in search of food. They are particularly fond of sweets, of which they may absorb considerable quantities, their gaster then becoming greatly distended. At Khartum, cases of œdema of the eyelids have been ascribed to the bites of ants (Chalmers, 1918). Yet even these domestic ants should not be considered wholly noxious, because many of them are to a large extent carnivorous, thus destroying great numbers of roaches, larvæ of flies, and other indoor pests (see Illingworth, 1913 and 1917). Perhaps the most dreaded of these house ants are the fire-ant, *Solenopsis geminata* (Fabricius), a very pugnacious species with a severe sting, and the Argentine ant, *Iridomyrmex humilis* Mayr, which is becoming a serious nuisance in many subtropical countries.²

By far the majority of ants afford to the vegetation a very effective protection, destroying a large number of phytophagous insects.³ Foremost in this respect are the driver ants (Ecitonini in America, Dorylini in the Old World tropics), with their populous colonies and wandering habits, and also the many, highly carnivorous Ponerinæ.⁴

The wandering armies of South American *Ecitons* have been described by H. W. Bates (1863, p. 354), Belt (1874, p. 17), and many others. Perhaps Richard Spruce's account (1908, II, pp. 370-373) gives the clearest idea of the usefulness of their operations and it is interesting enough to be quoted at length:

Ecitons or foraging ants (called Cazadoras in Peru) seem to be true wandering hordes, without a settled habitation; for a certain number of them may always be seen carrying pupæ, apparently of their own species; but they sojourn sometimes for several days whenever they come upon suitable food and lodging. . . .

The first time I saw a house invaded by Cazadoras was in November 1855, on the forest slope of Mount Campana, in the Eastern Peruvian Andes. I had taken up my abode in a solitary Indian hut, at a height of 3,000 feet, for the sake of devoting a month to the exploration of that interesting mountain. The walls of the hut were merely a single row of strips of palm trees, with spaces between them wide enough to admit larger animals than ants. One morning soon after sunrise the hut was suddenly filled with large blackish ants, which ran nimbly about and tried their teeth on everything. My charqui proved too tough for them; but they made short work of a bunch

¹*Pheidole megalocarpa* has of late been replaced as house ant in Madeira by the Argentine ant, *Iridomyrmex humilis*.

²Ants more commonly found in or near houses in India are, according to Assmuth (1907, p. 302), *Prenolepis longicornis* (Latreille) and *Monomorium pharaonis* (Linnaeus).

³The activity of ants in destroying noxious insects was discussed in detail by H. Stitz (1917) in a recent paper. Delpino (1875, p. 89) expressed the view that "the ants are the chief equilibrating and moderating factors affecting phytophagous insects," perhaps a somewhat overdrawn statement.

⁴Some of the African Ponerinæ are almost exclusively termitophagous. See, for instance, the accounts of the habits of *Megaponera futea* (p. 65), *Pallotyrus tarsatus* (p. 62), and others.

of ripe plantains, and rooted out cockroaches, spiders, and other suchlike denizens of a forest hut. So long as they were left unmolested, they avoided the human inhabitants; but when I attempted to brush them away they fell upon me by hundreds and bit and stung fiercely. I asked the Indian's wife if we had not better turn out awhile and leave them to their diversions. "Do they annoy you?" said she. "Why, you see it is impossible for one to work with the ants running over everything," replied I. Whereupon she filled a calabash with cold water, and going to the corner of the hut where the ants still continued to stream in, she devoutly crossed herself, muttered some invocation or exorcism, and sprinkled the water gently over them. Then walking quietly round and round the hut, she continued her aspersion on the marauders, and thereby literally so damped their ardour that they began to beat a retreat, and in ten minutes not an ant was to be seen.

Some years afterwards I was residing in a farm-house on the river Daule, near Guayaquil, when I witnessed a similar invasion. The house was large, of two stories, and built chiefly of bamboo-cane—the walls being merely an outer and an inner layer of cane, without plaster inside or out, so that they harboured vast numbers of cockroaches, scorpions, rats, mice, bats, and even snakes, although the latter abode chiefly in the roof. Notwithstanding the size of the house, every room was speedily filled with the ants. The good lady hastened to fasten up her fresh meat, fish, sugar, etc., in safes inaccessible even to the ants; and I was prompt to impart my experience of the efficacy of baptism by water in ridding a house of such pests. "Oh," said she laughingly, "we know all that; but let them first have time to clear the house of vermin; for if even a rat or a snake be caught napping, they will soon pick his bones." They had been in the house but a very little while when we heard a great commotion inside the walls, chiefly of mice careering madly about and uttering terrified squeals; and the ants were allowed to remain thus, and hunt over the house at will, for three days and nights, when, having exhausted their legitimate game, they began to be troublesome in the kitchen and on the dinner-table. "Now," said Dona Juunita, "is the time for the water cure"; and she set her maids to sprinkle water over the visitors, who at once took the hint, gathered up their scattered squadrons, reformed in column, and resumed their march. Whenever their inquisitions became troublesome to myself during the three days, I took the liberty to scatter a few suggestive drops among them, and it always sufficed to make them turn aside; but any attempt at a forcible ejection they were sure to resent with tooth and tail; and their bite and sting were rather formidable, for they were large and lusty ants. For weeks afterwards the squeaking of a mouse and the whirring of a cockroach were sounds unheard in that house.

In their general economy and behavior, the African Dorylini differ but little from the Ecitonini, as can be seen from various descriptions of their marauding columns quoted in Prof. Wheeler's Report of the Congo ants (pp. 46-49). It may, however, be noted that their armies are apparently much more populous than those of the ecitons and also more troublesome when invading human dwellings. A rather successful method of keeping them away from inhabited places consists in making a barrage of hot ashes across their highways.

Whoever has seen the almost fabulous numbers of individuals in the ant armies of the tropics can have no doubts as to the benefit they afford the vegetation by destroying caterpillars and other noxious insects. Since it is evidently the general impression that driver ants indiscriminately destroy all "pests" within their reach, I should like to call attention to some curious experiments with Dorylini made by Swynnerton (1916) in South East Rhodesia. His observations indicate how careful one must be in applying general formulæ to the interrelations of living beings. After giving an impressive account of the columns of driver ants (*Dorylus nigricans* variety *molestus* Gerstaecker) which "seize on any potential prey, from a minute beetle to a cow, that is so foolhardy as to approach them," Swynnerton describes with much detail his experiments to ascertain whether any non-flying insects are safe from these marauders. The unexpected conclusion was reached that these ants show strong preferences "readily taking some animals when they would not take others at all, and when failing in their attacks on yet others." Among the insects left unharmed by the ants of one of the columns were certain beetles (*Mylabris*, *Epilachna*) and caterpillars (*Amauris*, *Acræa*). "A small sciarid fly (*Apelmocreagis thoracica* Macq.) had been settled on the ground right amongst the ants, neither taking any notice of them nor drawing an attack. I captured and disabled it and placed it back amongst them, but tho numbers, I might say hundreds, inspected it, often passing their antennæ over it, all moved on and no attack whatsoever was made." The eggs and very young larvæ of most Rhopalocera experimented with were found to be quite unacceptable to driver ants.¹

Swynnerton's experiments, however, do not materially detract from the total of the highly beneficial activity of the driver ants which, indeed, are a blessing to all tropical cultures. As Vosseler (1905, p. 298) states, "in a given time they destroy more insect vermin than all other insect-eating animals (birds, lizards, turtles, frogs, spiders, etc.) together, since they clean out to a certain depth the entire field invaded by them." The invasions of these Huns of the insect-world should be welcomed by all agriculturists in tropical regions, even if their pugnacious character and great numbers make them troublesome at times to human beings and domestic animals.

In Europe, foresters generally believe, apparently with good reason, that trees which attract ants or are surrounded by ant nests are less

¹Members Lang and Chapin inform me that, according to their observations, driver ants are unable to take hold of the larvæ of *Dermestes*, evidently due to the abundant coating of hairs and also to the manner in which these larvæ can bend their body. They frequently witnessed the unsuccessful attempts of one or even several driver ants to grasp a *Dermestes* larva.

subject to the attacks of caterpillars and other noxious insects.¹ The very populous colonies of certain species of *Formica* prove most valuable in this respect. Forel has calculated that a large colony of the European *Formica rufa* daily destroys at least 100,000 insects. Certain plants possess various organs, such as nectaries and myrmecodomatia, which are often utilized by the ants. Whether these structures are intended merely to allure the ants which would thus form a body-guard to the plant, as Delpino and other botanists have believed, is a much discussed problem and will be considered more in detail elsewhere.

The protection afforded to the vegetation by many ants is so evident that it has been employed by some of the most progressive agricultural people, such as the Chinese and the Malays.² In Southern China and Indo-China it is an ancient custom to place the nests of certain insectivorous ants in the trees; in this way orange and mandarine trees are said to be kept free from caterpillars (McCook, 1882). Such use was recorded as early as 1640, and Emery identified the ant in question as *Ecophylla smaragdina*, the common silk ant or red tree-ant of the Old World tropics.³ The Javanese of certain districts use ant nests, again probably those of *Ecophylla*, to protect their mango-trees from fruit-boring weevils, *Cryptorhynchus mangiferæ* (Fabricius), and, in order to give the ants a broader field for their activities, the various trees of a plantation are connected by means of bamboos (Vorderman, 1895).⁴ The benefit derived from the presence of the predaceous *Ecophylla* is, however, partly offset by the fact that these ants usually keep coccids and peculiar caterpillars within their own nests, as shown by many observers (F. P. Dodd, 1902; Maxwell-Lefroy and Howlett, 1909, pp. 230-231; G. R. Dutt, 1912; Keuchenius, 1914a and 1914b).

Various attempts by agriculturists to make a more direct use of protection by ants have not thus far proved very successful. Perhaps many of these experiments have failed from lack of proper knowledge of

¹Ratzeburg, 1844, III, p. 42; 1866, I, p. 143; 1868, II, p. 429. Judeich and Nitsche, 1895, I, n. 717.
²Popenoe (1921) has recently called attention to the use of certain unidentified ants by the Arabs of Yemen to combat insects noxious to date-palma. He quotes P. E. Botta (1841, 'Relation d'un voyage dans l'Yemen,' (Paris), p. 155) who says he verified the fact and who credits Forskål with having first observed it about 1764. In Forskål's posthumous work, however, edited by Niebuhr (1775, 'Descriptiones animalium quæ in itinere orientali observavit,' (Copenhagen), p. 834, under the name *Formica animosa* the following rather obscure statement appears: "Welcome to gardeners because of the useful animosity with which it pursues the 'Dharr' ants perniciously infesting *Phariz dactylifer*. To this war it is led by heaping up 'Heml' (camel excrement) as its imperial reward." I have been unable to find additional information on this subject in Niebuhr's account of his travels with Forskål in Arabia (in Pinkerton, J., 1911, 'A general collection of the best and most interesting voyages and travels,' (London), X, pp. 1-221).

³Emery, C., 1889, p. 15 of separate. Emery received his specimens from Bangkok. Dr. C. W. Howard recently sent Prof. Wheeler ants used for similar purposes by the Chinese near Canton; they also belong to *Ecophylla smaragdina*.

⁴In the Congo the silk nests of *Ecophylla* are very frequently found in fruit-trees and in coffee and rubber plantations.

ant behavior. The Guatemalan kelep-ant, *Ectatomma tuberculatum* (Olivier), introduced some years ago into Texas for the purpose of exterminating the cotton boll weevil (*Anthonomus grandis* Boheman), apparently has not in any way helped control this ill-reputed pest.¹ *Solenopsis geminata* (Fabricius), the "fire-ant" of the warmer regions of the world, apparently is a much more powerful enemy of the boll weevil (W. D. Hunter, 1907; W. E. Hinds, 1907). In certain parts of Brazil, the "formigas cuyabanas," *Prenolepis fulva* Mayr,² are considered very effective in fighting the leaf-cutting ants ("saúvas" or Attini), though there seems to be but little foundation for this belief (H. v. Ihering, 1905 and 1917; A. da Costa Lima, 1916). F. v. Faber (1909) claims that in Java "a black ant, 3 to 4 mm. long," but not otherwise identified, successfully controls the bugs of the genus *Helopeltis* in cacao plantations. Perhaps this is *Dolichoderus bituberculatus* Mayr, an ant which, according to de Lange (1910) and Moorstatt (1912), is used in Java to combat these same *Helopeltis* of cacao.

According to Rothney (1889, p. 355), two ants, *Monomorium salomonis* (Linnæus) and *Solenopsis geminata* (Fabricius), are deliberately introduced into warehouses in Madras to check the depredations of white ants. "This practice is not uncommon in Northern India and the natives of India are familiar with the kind of ant which should be brought in" (Maxwell-Lefroy and Howlett, 1909, p. 226).

Another service of ants which should not be overlooked by ecologists is their ceaseless activity in excavating, transporting soil particles, and hastening the decay of organic substances. Their multiple burrows, extending in all directions underground, bring about a very thorough ventilation of the soil and an easy and even distribution of moisture. They comminute and bring to the surface a large quantity of soil and subsoil, often from a considerable depth, and leave it exposed to the weathering action of the meteoric agents. Furthermore, they introduce into their subterranean excavations much organic matter which thus more readily decays and in turn yields acids that act upon the soil.

Owing to the hidden habits and minute size of most ants, their importance as geologic agents may be easily lost sight of, especially in temperate regions. In tropical and subtropical countries the result of their toil is often much more apparent, though it rarely approximates

¹See various papers by O. F. Cook (1904, 1905, and 1906) and their criticism by Wm. M. Wheeler (1904, 1905a, and 1906). A list of ants known to prey on the cotton boll weevil is given by W. Pierce (1912, pp. 69-73).

²Also called "*formigas cearenses*" or "*formigas paraguayas*"; various other species of ants are occasionally taken for "*cuyabanas*."

that produced by termites. Only certain species of *Formica* in temperate Europe and North America construct mound or hill nests of sufficient size or number to attract much attention; with them, the accumulations consist of a small part of excavated soil, most of the material being gathered in the vicinity by the workers. The conical mounds of the North American *Formica exsectoides* sometimes reach a meter in height and two to three meters in diameter at the base, while those of the European *F. rufa* often are much larger (over two meters high and eight to ten meters in diameter).

The crater-shaped or conical mounds of certain North American harvesting ants are partly made of earth brought from underground excavations. Those of *Pogonomyrmex barbatus* subspecies *molefaciens* may attain one to two meters in diameter and fifty centimeters in height, while in the common *P. occidentalis* they are but little smaller and often form extensive colonies (Headlee and Dean, 1908; Wheeler, 1910). *Ischnomyrmex cockerelli*, of the southwestern United States, surrounds the entrance to its nests with huge craters, from sixty centimeters to two meters in diameter and from 0.2 to 0.5 centimeters in height, built of coarse desert soil intermingled with pebbles sometimes two centimeters in diameter (Wheeler, 1910, p. 281).

The volume of material moved by some of the leaf-cutting ants (Attini) of tropical America is much greater than in any of the cases mentioned above. H. v. Ihering (1882), Gounelle (1896), and Branner (1896, 1900, 1910, 1912) have called attention to the importance of these insects as geologic factors. In certain parts of Brazil the ant hills of the saúva (*Atta* species, probably *cephalotes*) are so large and numerous that they become a remarkable feature of the landscape. At one place in the Rio Utinga region, in the interior of Bahia, where the forest had been cleared away so that the mounds were visible, Branner counted fifty-three of them within an area of 10,000 square meters. Their bases covered close to one-fifth of the total space under consideration and their volume was estimated at 2225 cubic meters. The cubical contents of the mounds, if evenly distributed over the entire 10,000 square meters, would have been 22.25 centimeters thick. In this case, the height of the ant hills varied from 1.2 to 4.5 meters, with an average of 2.5 meters. These were not the largest seen, for on the upper drainage of the Rio Utinga, Branner measured mounds of leaf-cutters five meters high and sixteen or seventeen meters in diameter at the base, each containing about 340 cubic meters of earth. The illustrations in Branner's latest papers (1910, 1912) remind one of strikingly similar landscapes with scattered termite

hills in many parts of tropical Africa (see Pl. XV). A considerable amount of living vegetable matter is carried by the leaf-cutting ants into the inner chambers of their nests, where it is cut up and worked in their mushroom-beds; vegetable substance is thus rapidly transformed into mineral matter and rendered available to new plant-growth.

True mound- or hill-building ants are not found in tropical Africa; many species, however, build small crater-shaped accumulations of earth at the entrance to their nest. Those of the seed-storing *Messor* are often very conspicuous in the arid parts of the continent; their craters sometimes measure a meter or more across and the earthen walls may reach twenty-five centimeters in height (Passarge, 1904, pp. 290-295; see also the photograph of a nest of *Messor* species taken by Mr. Lang on the Athi Plains, British East Africa, Pl. XXVI, fig. 1). The driver ants, when establishing their temporary abodes, often excavate considerable quantities of soil, as is shown by Mr. H. Lang's photograph of a nesting site of *Dorylus* (*Anomma*) *wilverthi* Emery (Pl. II).

The following chapters deal with many other activities by which ants come into direct contact with plants. They will further emphasize the importance of ants in the economy of nature, in which they must undoubtedly be regarded as the dominant insects (Wheeler). From the narrow point of view of human interests, by far the greatest number of ants are indifferent or negligible organisms, either because of their small size and scarcity of their colonies, or because they avoid the vicinity of man's activities. With regard to the comparatively few species that are of economic importance, "a consideration of all the facts forces us to admit, with Forel, that as a group ants are eminently beneficial and that for this reason many species deserve our protection. Some of our species, however, are certainly noxious, and these offer strong resistance to all measures for their extermination, owing to the tenacity with which they cling to their nesting sites, their enormous fertility and the restriction of the reproductive functions to one or a few queens that are able to resist destruction by living in the inaccessible penetralia of their nests" (Wheeler, 1910, p. 8).

Ants as Agents in the Pollination of Flowers

In Knuth's celebrated 'Handbook of Flower Pollination'¹ ants are dismissed with the brief statement that they "frequently occur as ravagers of flowers, for which reason Læw has termed them *dystropous*."

¹English translation. Oxford, 1906, I, p. 168.

Perhaps even in temperate zones this is not entirely true, and it is difficult to believe that, in Umbelliferae and other flower associations with freely exposed nectar on which ants are most commonly met with, these insects are not at least effective agents of geitonogamy. In the tropics, moreover, ants are so abundant everywhere that very likely they are of even greater importance as carriers of pollen, the more so since many trees and shrubs of tropical forests bear flowers on their old wood on the very highways of the ants, so to speak. One might even venture to suppose that cauliflory is mainly of use to the plant in that the flowers are thus placed within easy reach of pollinating ants. Indeed, the question as to the origin and significance of cauliflory in tropical trees and shrubs has not thus far been satisfactorily answered. Wallace¹ regards it as an adaptation to pollination by butterflies, which, he says, keep to the undergrowth of the forest and rarely ascend to the crown of the trees. Haberlandt (1893, p. 132) argues that many of the caulinary flowers are dull colored and also otherwise but little adapted to Lepidoptera, and, from my personal experience in the Ituri forest, I must agree with him. I cannot recall a single instance in which I saw caulinary flowers visited by butterflies and I greatly doubt whether Wallace's explanation was founded on actual observation. In Haberlandt's opinion, cauliflory is merely the result of a tendency to a more complete division of labor, resulting in a sharper differentiation between the assimilating and the reproductive parts of the plant. Evidently A. F. W. Schimper (1903, p. 338) is also satisfied with a mere physiological solution when he supposes that the frequent occurrence of cauliflory among tropical trees is due to a weaker development or slighter degree of roughness of the bark.

The foregoing remarks will suffice to show that the relations between ants and cauliflorous plants are worthy of further attention. In his biological studies of tropical flowers, H. Winkler (1906) enumerates a number of plants in Cameroon which he asserts are pollinated by ants, though he does not enter into details nor describe any adaptations of the flowers to this peculiar mode of fecundation. It is interesting to note that most of the species thus mentioned by Winkler are cauliflorous trees or shrubs. The cacao tree (*Theobroma Cacao*) affords a classical illustration of cauliflory, its flowers being borne on both stem and main branches; in this case G. A. Jones (1912), from his experiments carried on in Dominica, West Indies, has reached the conclusion that ants are in all probability the chief agents of pollination.

¹1891, 'Natural selection and tropical nature,' (London), p. 244.

H. N. Ridley (1910, pp. 461-462) has made some interesting observations in Singapore on certain species of the anonaceous genus *Goniothalamus*, notably *G. Ridleyi* King, which produce their flowers in masses at the base of the tree.¹

The flowers are of large size and dull reddish in color. They are almost invariably covered by a nest of very small black ants, which pile up powdery soil all over them, so that they are often quite concealed. It would, I think, be difficult for a bee or other insect to get to the honey of these flowers through the nest, yet I think no species of the genus fruits so regularly or heavily as does *Goniothalamus Ridleyi*. That the ants are distinctly attracted by the flowers, is clear from the fact that the flowers from the trunk which are too high up for the ants to cover with the nest are generally densely covered by a swarm of the insects. Owing, however, to the minuteness of the ants and the difficulty of making observations in such a mass of them, I have been unable to definitely decide whether the ants do actually fertilize the flowers by conveying the pollen from one to the other, but I can not see any other way in which the fertilization can be effected. The ants generally throw up the mounds over the flowers before the buds open, as if in anticipation of the honey within the flowers. In most species of the genus the flowers are borne on the branches or upper part of the stem, and are brighter in color, white or orange, and these are not haunted by ants, but doubtless fertilized by hymenopterous or dipterous insects. If the flowers of *G. Ridleyi* are, as I believe, fertilized by ants, their position at the base of the stem may be taken as a modification to that end. This, however, could not be classed as symbiosis, but rather as a modification for fertilization, as the main nest of the ants is apparently always underground near the tree.

Ants and Extrafloral Nectaries

Under the term "extrafloral nectaries" botanists include all glands secreting saccharine substances located on the vegetative organs of plants, while the "floral nectaries" are similar nectar-secreting glands found on parts of the flower or of the inflorescence.² There is still considerable discussion as to the true significance of nectaries. In this connection it is rather interesting to observe that all earlier botanists regarded even the floral nectaries as having a physiological function. Some believed that the saccharine secretion accumulated in the flowers served to feed the embryo; others considered the nectaries as excretory organs, eliminating waste substances of no further use or perhaps even noxious to the plant. In later years the majority of naturalists have accepted none but an ecological explanation. That the nectar glands of

¹M. S. Evans (1876) has described cross-pollination by means of ants in an unnamed rubiaceous shrub on the coast of Natal.
²Delpino (1874 and 1875c) proposed to replace these terms with "extranuptial" and "nuptial" nectaries respectively. A "nectary" was originally defined by Linnaeus (1751, *Philosophia botanica*, p. 53), as that part of the flower which produces the honey: "*nectarium, pars mellifera floris propter*" Caspary (1848, *Denkschriften, Tierfeld*) apparently first made the distinction between floral and extrafloral nectaries. The historical side of the question has been fully treated by G. Bonnier (1879).

flowers attract pollinating insects, which in turn assure or greatly facilitate cross-fertilization, is too well established a fact to be doubted. It is, however, by no means certain that these floral nectaries are not at the same time more directly useful to the plant in a physiological way.¹

Ants are frequently seen busily visiting the extrafloral nectaries of certain plants. They are, for instance, seldom absent from the large stipular glands of certain species of *Vicia* (*V. sepium*, *V. sativa*, and *V. Faba*) in Europe (see Rathy, 1882, pp. 29-36; Hetschko, 1908). In North America the stipules of some species of *Cassia* are especially attractive to these insects. In the Belgian Congo, I have taken numbers of ants, together with many other Hymenoptera and Diptera, as they were sucking up the sweetish fluid secreted at the base of the leaf-blade of *Urna lobata* variety *reticulata* Guerke, a very common weed in native villages and cultures.² The foliar nectaries of several Javanese species of *Hibiscus* are also very inviting to ants (Kœrnicke, 1918). It is on similar observations that Delpino (1874, 1875, 1879), A. F. W. Schimper (1888), and Kerner von Marilaun (1876) based their ecological interpretation of extrafloral nectar glands. The following passage from Delpino's earliest paper (1874, pp. 237-238) may be reproduced in full, as it sums up his views:

What then is the function of the extranuptial nectaries, which are found on the caulinary leaves, on the bracts, and on the calyx? Though I reserve for another paper the publication of my studies of such and other extradihogamic relations between plants and insects, I do not hesitate to announce now that the chief function of these nectaries is to place the ants, wasps, and *Polistes* in the position of sentries and guards, to prevent the tender parts of the plant from being destroyed by larvæ. Where ants and wasps are present, larvæ cannot exist because they will be devoured. Thus certain plants have adopted the same means of defense and bait that we see used by the tribe of aphids, coccids, *Tettigometra*, and other cicadellids, which spontaneously place themselves under the powerful protection of ants. Still another function, though a subordinate one, can sometimes be carried on by the above-mentioned nectaries, namely that of keeping the ants from the nuptial nectaries by detaining them at the extranuptial nectar glands. Indeed we can ascertain the noxious effects of ants when they succeed in infesting the flowers. In the first place, ants have sedentary habits, remaining motionless for whole hours on the same flower: therefore, they are of no use in dichogamy. Secondly, ants are objects of fright and aversion to the natural pollinating insects of the plant, as for instance, flies, butterflies, and bees; hence, their presence on the flowers renders useless the dichogamic devices of these plants. I have repeatedly observed bees and humble-bees avoid visiting flowers when they saw ants there. Which all makes it clear how plants under given circum-

¹G. Bonnier (1879, p. 206) after a critical study of the subject, from an anatomical and a physiological viewpoint, concludes: "The nectariferous tissues, whether floral or extrafloral, whether or not producing a liquid externally, represent special food reserves directly connected with the life of the plant."
²See my notes on this plant in *Rev. Zool. Afr.*, III, fasc. 1, 1913, p. 3.

stances may find great profit in producing extranuptial nectaries, either to secure permanent and bold guards against the invasions of larvae or to lure the ants away from the flowers.

In some of his later publications Delpino has even proposed that all plants with extrafloral nectaries be regarded as myrmecophytes, and has followed this course in his elaborate 'Monograph of the Myrmecophilous Function in the Vegetable Kingdom' (1886-1889). Such an extreme view has not been accepted by many other naturalists, probably because it would extend the concept of myrmecophytism to include a very considerable portion of the world's flora.¹

A. F. Schimper and Kerner von Marilaun fully endorse Delpino's theory and endeavor to give further evidence in its support. Kerner, for instance, has a clever explanation of how the involueral nectar glands of certain Compositae attract ants which defend the capitula against voracious beetles.² He has also built further on the idea that the extrafloral nectaries keep ants away from the flowers where they would come as "unbidden guests" to feed on the floral nectar without aiding in cross-pollination. He claims that ants climbing the plant thus find on their way up an ample and readily accessible supply of honey, and consequently do not trouble to go to the flowers.

Many objections can, however, be raised to Delpino's theory. First, myrmecologists will not readily admit Kerner's supposition as to the limitation of the ants' feeding propensities. As a matter of fact, these insects are sometimes found inside flowers of various types, and frequently so on those with freely exposed nectar, such as the Umbelliferae. In tropical regions at least, as I have suggested above, they should not be wholly disregarded as pollen carriers. Secondly, observation shows that the extradoral nectaries, while present in a great number of species, are in many of them seldom if ever visited by ants. Thirdly, the visitors of extrafloral nectar glands especially attractive to insects frequently do not consist of ants only, but include various other Hymenoptera, Diptera, and Coleoptera, which are by no means deterred by the ants.³ And lastly, it has not been sufficiently well established that the

¹O. F. Cook's papers on the "kelep" ant offer a typical example of the lengths to which "myrmecophilum" may be carried by certain naturalists. According to this author (1904 c, p. 660) the cotton-plant of eastern Guatemala has, through its extensive system of extrafloral nectaries, secured the active cooperation of the kelep or weevil-eating ant, *Ectatomma tuberculatum* (Olivier), against the boll weevil!

²The nectar glands at the involueral bracts of certain Compositae have been further investigated by v. Wettstein (1888) and Hetschko (1907). The last-named observer found that the sweet excreting bracts of the European *Centaurea montana* Linnæus are visited not only by ants (*Myrmica larinodia*, *M. ruginosa*, and *Lasius niger*) but also by other Hymenoptera (Apidae, Vespidæ), Diptera, and Coleoptera.

³Hetschko (1908) gives a list of the visitors he observed at the stipular nectaries of *Ficus aspera* Linnæus. It includes, in addition to four ants (*Formica rufa*, *F. ruginosa*, *Lasius niger*, and *Myrmica larinodia*), 21 species of Hymenoptera (6 Apidae, 4 Vespidæ, 2 Sphegoidea, 10 Ichneumonidae, and 2 Tenthredinidae), 21 of Diptera (8 Syrphidae, 12 Muscidae, and 1 Hibernidae), 8 of Coleoptera (3 Cantharidae, 2 Heteroceridae, 1 Phalacroderma, and 2 Coccinellidae), and 1 of Hemiptera.

presence of the "body-guard" of ants actually favors the species or individual plant on which they are found, though it cannot be denied that, when present in large numbers, they give to the plant a certain amount of protection.¹

The so-called "food-bodies" of the myrmecophytes *Acacia sphaerocephala* (Beltian bodies) and *Cecropia adenopus* (Müllerian bodies) are probably also of glandular origin (F. Darwin, 1876); they are described in my synopsis of the myrmecophytes (p. 503). Such structures are by no means restricted to certain typical ant-plants. *Leca hirsuta* Blume, a common Javanese bush of the family Ampelidaceae, produces spherical excrescences on the tender parts of the plant, in abundance on the young petioles, also on the young leaf-blades near the midrib and on the stem of young shoots. These glandular bodies, about 0.7 mm. long, consist of an outer layer of small cells enclosing much larger cells filled with oil drops and albuminoid granules. They are eagerly collected by ants and consequently often difficult to find on the plant (Raciborski, 1898). A similar case is that of *Pterospermum javanicum* Junghuhn, one of the Sterculiaceae in Java, which bears in its funnel-shaped stipules minute food-bodies also collected and carried away by ants (Raciborski, 1900). In both these cases other species of the same genus lack these food-bodies completely. Since neither *Leca hirsuta* nor *Pterospermum javanicum* possesses myrmecodomatia, they could not well be regarded as true myrmecophytes, no more than the many plants which are merely provided with extrafloral nectaries. Their case offers a suggestive comparison with the Müllerian and Beltian bodies and weakens the argument that the last-named growths are myrmecophilous organs connected with the presence of ant-dwellings in *Cecropia adenopus* and *Acacia sphaerocephala*.

It thus seems that, from the point of view of the myrmecologist, extrafloral nectaries and "food-bodies" are little more than additional sources of food which ants are so keen in detecting and in exploiting to the very limit. All ants are fond of sweets and this is especially noticeable in species with a vegetarian or semi-vegetarian diet. In many cases the sugary juices are absorbed so eagerly by the workers that their crop distends considerably and the gaster is temporarily inflated to a size entirely out of proportion to the rest of the body. Extreme instances of the kind are the so-called "honey ants" of the arid plains and deserts of North America, South Africa, and Australia. In certain ants of these

¹A comprehensive criticism of Delpino's theory of extrafloral nectaries has been given by Mrs. M. Nieuwenhuis von Uxkull-Göldenbrandt (1907).

regions some individuals of the worker caste have developed into a special form of "repletes," which act as living reservoirs of liquid food for the purpose of tiding over periods of scarcity. Their "honey" is obtained from the excretions of various Hemiptera (see p. 336) and the sweet exudations of different plant organs and even of certain galls. A few years ago Wheeler published a complete account of the honey ants (1908b and 1910b, pp. 361-377), to which but little can be added at present.

Repletes have been described for the African *Plagiolepis trimenii* Forel,¹ discovered by Hutchinson in Natal. They are 6.5 mm. in length, of which the head and thorax together measure only 2 mm., and are said by Forel (1895) to have their gaster "distended with honey, like a round cyst, transparent, as large as a hemp seed, on which the chitinous laminae of the segments appear like islands. The anterior portion of the first segment has a hollow depression into which the petiolar scale fits. With the aid of a lens it is possible to distinguish, below and behind, the stomach and gizzard with its reflected calyx, both of them displaced and flattened against the gastric wall." The gaster in these repletes is, according to the same author, nearly as fully distended as that of the North American *Myrmecocystus melliger*, and locomotion must be almost impossible for this insect.

The habit of using some of the members of the colony as honey pots will probably be discovered in certain other ants of the African deserts. Among other species it may be still in an incipient stage, as, for instance, in the case of *Acantholepis arnoldi* Forel in Southern Rhodesia. The nests of this ant are found in loose, sandy soil in the hottest places. They sometimes contain workers with gaster considerably swollen, as long as the head and thorax together, but not so rotund as in the repletes of *Myrmecocystus* or *Plagiolepis trimenii* (Arnold, 1920, p. 564).

Dispersal of Seeds by Ants

That certain ants gather seeds and preserve them in special granaries in their nests has been known since very ancient times. There are frequent allusions to harvesting ants, and even more or less accurate accounts of their activities, in the writings which have come down to us from the older civilizations along the shores of the Mediterranean.² Yet such keen myrmecologists of western Europe as Latreille and P.

¹*Plagiolepis decolor* Emery, a very closely allied South African species, is, according to Forel, also a honey ant.

²These old accounts are given in the works of Moggridge (1873, pp. 5-11) and McCook (1879a, pp.

Huber, unacquainted with the spectacular seed-storing habits of certain southern ants, discredited the assertions of the ancient writers. Though Sykes (1835) and Jerdon (1851) in India and Buckley (1861a) and Lincecum (1862) in North America had actually observed certain ants collecting large quantities of seeds, it needed the careful investigations of Moggridge (1873) in southern France and of McCook (1877 and 1879a) in Texas to dispel the skepticism of modern entomologists.

It is only more recently, however, that naturalists have come to appreciate the general importance of ants as seed distributors. Their rôle in this respect seems to have been first realized by Kerner von Marilaun (1895, pp. 866-867). Later F. Ludwig (1899, p. 38) definitely asserted that "ants do not only aid in scattering plant seeds, but that they play a prominent part in the dispersal of the indigenous (European) vegetation." In Sernander's comprehensive 'Monograph of European Myrmecochores' (1906b) one finds a detailed and critical history of the subject, together with an immense array of new and interesting observations. His conclusions show that in Europe a great many grasses and herbaceous plants rely almost exclusively, or at least to a large extent, on certain species of ants for the successful scattering of their seeds. Many of the more common ants, belonging to such ubiquitous genera as *Formica*, *Lasius*, *Tetramorium*, and *Myrmica*, gather seeds of various plants more or less consistently. To the phytologist these widely distributed ants are perhaps factors of greater importance than the true harvesters. The latter, to be sure, are more spectacular in their performances, but they are restricted to certain desert or semi-arid regions and are evidently extreme cases, remarkable for the huge quantities of seeds stored in their granaries.

The ecological significance of seed-transporting ants can only be adequately realized upon closer scrutiny of the actual results of their activity in this line. Sernander's calculations, though based on moderate figures, show that the amount of seeds carried about by ants must be considerable. He found, for instance, that a single colony of *Formica rufa* transports during one season about 37,000 seeds and fruits. Observation also discloses that the seeds are in this way conveyed appreciable distances (100 to 200 feet) from the mother-plant. On their foraging excursions ants frequently drop or lose seeds along the road. Furthermore, many of the seeds finally stored in the recesses of the nest are sooner or later cast out near the entrance along with chaff and other débris from the ants' household, and a number of them are still able to germinate. Finally, with further investigation, the number of myrme-

cochores, or species of plants whose seeds are garnered by ants, increases steadily.¹

One might reasonably surmise that in tropical countries too ants will be found to be efficient agents in the dispersal of the seeds and fruits of many species; but, as yet, this side of tropical ant behavior has been barely touched upon. O. Kuntze (1877, p. 24) mentions incidentally that in South America he saw ants carry off the seeds of papaw-trees (*Carica Papaya* Linnæus). R. H. Lock (1904) gives a short account of the dispersal in Ceylon of *Turnera ulmifolia* Linnæus by ants (*Pheidole spathifera* Forel) which are apparently attracted by the arillus of the seed. More recently, W. and J. Docters van Leeuwen-Reynvaan (1912) have carefully investigated the scattering of the seeds of *Dischidia Rafflesiana* Wallich and *D. nummularia* R. Brown, which are common epiphytes in Java. The pappiferous seeds of these Asclepiadaceæ bear a narrow, white caruncle of thin-walled cells filled with fatty and albuminous substances. When the fruits are ripe, they split open and the seeds are carried away by the wind; if they lodge on a branch or trunk, they germinate when sufficiently moistened, but such seedlings do not develop into adult plants. Plenty of healthy seedlings can, however, be found in the galleries of *Iridomyrmex myrmecodia* Emery, an ant which builds its nest on and in the bark of trees. Moreover, this ant has been seen in the act of transporting *Dischidia* seeds, to which it was probably attracted by the caruncles. These minute ants, being unable to grasp the seed itself, pull off the longer, fragile hairs of the pappus and by means of the shorter, stronger hairs, drag the seed into a slit in the bark or among the roots and stalks of other *Dischidiæ*. It may be noted that in Java the pitcher-shaped leaves of these species of *Dischidia*² are usually inhabited by the same *Iridomyrmex*, so that this is perhaps one of the clearest examples of true symbiosis between ants and plants. It would be important to investigate further whether the ants actually feed on the caruncles of the seeds. The case of *Dischidia* also suggests comparison with the "ant gardens" of the Amazon, which are considered in more detail elsewhere (p. 365).

Ule (1900, p. 123) records finding the pea-sized seeds of *Ipomœa pes-capræ* Linnæus lying in long rows on the sandy sea-shore at Copaca-

¹Speaking of the seed-transport by *Messor barbarus* in Arbe, an island in the Adriatic Sea, F. Neger (1910a, p. 139) writes: "If one would draw up a list of all the plants whose seeds or fruits are carried by *Messor* into its nests, this list would almost be equivalent to an enumeration of the flowering plants occurring on the island."

²Ridley (1910, pp. 462-465) concludes that *D. Rafflesiana* cannot be regarded as a true myrmecophyte, but the relations between the ants and the seeds of this plant escaped his notice, so that the question will bear still further study.

bana, near Rio de Janeiro; he saw leaf-cutting ants (*Attini*) moving along, each carrying one of the seeds into a hole. It would thus seem that the *Attini* also store seeds in their nests or perhaps use them in their fungus gardens.

H. Winkler's (1906, pp. 236-237) statements concerning the dispersal of seeds by ants in Cameroon do not enter into much detail and merely show that the rôle played by ants in this respect in tropical Africa should not be disregarded. He says that in the dispersal of "numerous dry fruits with small seeds, ants are undoubtedly also of significance, since no spot in the tropical Rain Forest is free from these insects. I have almost always found that the arilli on dropped seeds of *Blighia* and other Sapindaceæ had been eaten away by ants. I have, however, never seen flower-gardens (due to ants) in Cameroon."

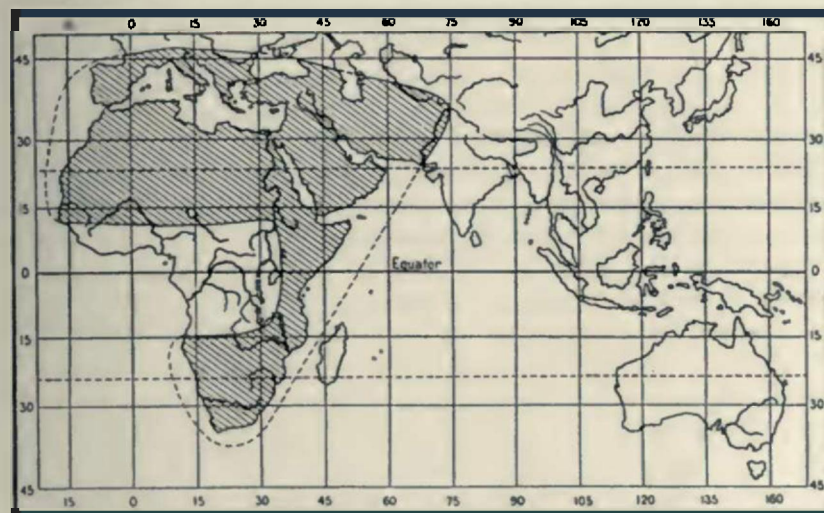
Harvesting Ants

The reader will find a complete review of this fascinating subject in the chapter devoted to harvesting ants in Prof. Wheeler's ant-book (1910b, pp. 267-293). The following account, therefore, will deal with what little is known at present of the seed-storing ants in the Ethiopian Region.¹

The typical Old World harvesters of the genus *Messor* are at home in the desert and semi-arid parts of the southern Palearctic, of the Ethiopian, and of the Indian Regions (Map 45). It is noteworthy that in Africa these ants, though widely distributed over the dry parts of the continent, avoid the moist West African Region (Engler's Western Forest Province), where seed-storing on a large scale is rendered practically impossible by the great moisture which prevails throughout the year, or at least for long periods, and would soon cause the stored seeds to sprout. Though *Messor* occurs as far north as Mossamedes and Bulawayo, as far west as the Great Rift Valley, and has recently been taken at Fort Crampel, French Congo, it has not been recorded from anywhere within the Congo Basin; yet it is not impossible that some of its forms might be found in Katanga. In East Africa this genus has the same general habits as in the Mediterranean Region (see Moggridge, 1873), as far as can be gathered from Sjöstedt's account of *Messor cephalotes* Emery, observed by him at the northern foot of Mt. Kilimanjaro:

¹Additional observations on the harvesting ant *Messor barbarus* subspecies *meridionalis* (Ern. Andre), in Macedonia, have recently been published by F. D. Döfler (1920).

At several spots one could see cleared spaces amidst the dry grass where every grass-stalk had been removed and the red-brown soil lay open to view, plane and clean as a well-attended garden plot. Such places were somewhat variable in size, mostly up to about 6 paces across and nearly circular. Heaps of fine grass-stalks cut to pieces (one to several liters; often 2 to 3 cm. long), together with grass panicles, were lying around. Scattered ants were wandering all over the place, the soldiers being especially striking on account of their big heads. The cleared place showed a large entrance, often more than finger-wide, into which the ants were dragging the stalk cuttings; more in particular I saw soldiers disappear with such cuttings through the entrance. The largest space I saw was 8 paces in diameter, with 4 or 5 separate entrances, one of which was larger than the others (as is the rule when there are many) and surrounded by an irregular, funnel-shaped depression, 15 to 20 cm. deep. The heaps of stalks, elsewhere clean and free from earth, were in this case mixed with soil and did not look as clean as usual. There were also holes in places along the path, into which the ants were dragging grass-stalks cut to pieces." (Mayr, 1907. pp. 14-15.)



Map 43. Distribution of *Messor*, a genus of harvesting ants. A subspecies of *M. barbarus* has recently been described from Fort Archambault, at about 9° 5' N., 18° 35' E.

Figure 1 on Plate XXVI represents one of these nesting sites of East African *Messor* from a photograph taken by Mr. H. Lang in the Athi Plains, British East Africa, during the R. Tjäder Expedition (July 1906). It is interesting to learn from Sjostedt's experience with *Messor cephalotes* in East Africa and that of Neger (1910a) with *M. barbarus* in southern Europe that certain species of the genus *Messor* are leaf-cutting. What use these ants may have for the plant cuttings in their nests is as yet unknown.

According to K. Escherich (1911a, pp. 48-51) *Messor barbarus* in Eritrea stays within its nests in the daytime, coming out in numerous columns after sunset to cut off panicles of grass and collect seeds, which are taken home; often pellets of earth or little stones are carried away by mistake. A few workers were also dragging bulblets of a *Cyperus*, probably *C. bulbosus*, which are in this way effectively scattered.¹

The genus *Pheidole*, abundantly distributed over all tropical and warm temperate regions of the world, is so closely allied to *Messor* that both have been included by Emery in one tribe, the Pheidolini, which also contains many other harvesting genera (*Oxyopomyrmex*, *Goniomma*, *Novomessor*, *Veromessor*, etc.); thus the seed-storing behavior is to some extent rooted into the phylogeny of the group. Certain Indian *Pheidole*, such as *Pheidole providens* (Sykes), are famous as harvesters, and many other members of the genus are also more or less granivorous. Mr. H. Lang and I discovered a typical seed-storing species, *Pheidole saxicola* Wheeler, in the Lower Congo. At Zambi the nests of this ant were placed in the interstices of stones on a rocky hill as shown on Plate VII and described by Mr. Lang in his field-notes (p. 139). From the debris, heaps of chaff, and rejected seeds thrown out by the ants and accumulated near the entrances of the nest, it was seen that the seeds gathered by this *Pheidole* belong chiefly to a few common grasses, such as *Chloris polydactyla* Swartz and various species of *Andropogon*. Concerning the genus *Pheidole*, Arnold (1920, p. 416) remarks that the South African species "are omnivorous, with a marked fondness for sugary substances, but some species, e. g. *excellens*, *crassinoda* and *arnoldi*, are mainly graminivorous, harvesting the seeds of grass in the same way as the species of *Messor*." *P. zocensis* Forel and its variety *bulawayensis* Forel are also mentioned by Arnold (1920, p. 445) as being "at least partly graminivorous, as the nests contained accumulations of grass seeds."

According to Arnold's observations, the commonest harvesters in South Africa are various forms of the genus *Messor* and certain species of *Tetramorium*. In his 'Monograph of the Formicidæ of South Africa' (1920, pp. 409-410), he writes of *Messor capensis* subspecies *pseudo-ægyptiacus* (Emery) as follows: "This variety is very common in the neighborhood of Bulawayo. It is eminently a harvesting ant, usually collecting the seeds of one particular kind of grass. The rejected husks of these seeds are deposited in a circle all around the entrance of the nest,

¹The bulblets of *Cyperus bulbosus* Vahl and *C. esculentus* Linnæus are also occasionally eaten by certain African natives.

one-half of the circle being generally deeper than the other, which may be due to the prevailing winds. These rubbish heaps when made by a populous colony sometimes reach very large dimensions, covering as much as one square foot of ground, and from one to three inches deep. The site of such a nest is very plainly indicated by these accumulations, since the husks are bleached almost white by the action of the sun. The nests of this ant appear to be very free of myrmecophilous insects and even the ubiquitous thysanuran is rarely to be found in them. The ants appear to have definite foraging grounds, to which access is obtained by well-marked and smooth paths leading from the nest in various directions." *Tetramorium setuliferum* Emery he describes (1917, p. 291) as "a harvesting and granivorous species. The entrances to the nests are often surrounded by small accumulations of husks of a grass seed. These heaps are smaller than those of *Messor*, and much less tidily disposed."

The ponerine ants are well known for their predaceous habits and highly carnivorous diet. Yet one at least of these ants, the common African *Euponera sennaarensis* (Mayr), is to a large extent granivorous. Arnold (1913, p. 13; 1915, p. 7) found that the nest of this species in Rhodesia "often contains considerable accumulations of grass seed which may be used as food," though this ant is also a keen hunter of termites. Similar observations have been made on this species by K. Escherich in Abyssinia (Forel, 1910, p. 245) and by myself in Katanga (Bequaert, 1913, p. 421).

There is little doubt that certain ants derive at least part of their sustenance from the seeds which they carry into their nests. Yet it is by no means clear how they manage to utilize the various amylaceous, nitrogenous, and oily substances contained in the seeds, either for their own nourishment or as food for their brood. In the case of the many widespread species which use seeds only in small quantities, as an additional food supply, it would seem that the caruncle alone is bitten off, neither the coats of the seeds nor their contents being touched. This is, however, not the case with true harvesters, some of which have become almost purely granivorous and, as a rule, remove the entire kernel of the seed. In his experiments with a colony of *Messor structor* kept in an artificial nest, Emery (1899 and 1912b) found that this ant would more or less readily accept cooked or dried meat, various fresh mushrooms, husked rice, a variety of ripe and unripe seeds, plant buds, bread, and dry vermicelli. These substances would all be to a certain extent triturated

between the mandibles, and finally a large or small quantity of residue would be dumped out of the formicary; but the ants steadily refused raw starch.

Emery also made some feeding experiments with a colony of *Messor barbarus minor* kept in an artificial nest of the Janet pattern. He found that this ant is less omnivorous than *M. structor*. It shows a predilection for dead insects; seeds rank only second in its choice, though they often constitute its principal food. When a ripe, dry, and unsprouted grain of wheat is offered to this species, the ants carry it into their nest and sooner or later gnaw off the embryo, always beginning to eat the grain at that end. This curious habit was even known to the ancient writers (Plutarch and others) who consequently attributed to the harvester ants a most wonderful instinct of preventing the sprouting of the grain by removing the germ. Emery, however, has shown experimentally that this is due merely to a matter of taste or gluttony manifested by the ants for this daintiest part of the grain. He believes that the ants mutilate the radicle of sprouted seeds for a similar reason, though he admits that this behavior may be of a more complicated nature.

Harvester ants can thrive perfectly on unsprouted grain, as shown by Emery's experiments, but in most cases they allow a partial germination of the seeds before using them as food. Neger (1910a) found that most of the seeds which *Messor barbarus* places in the sun near the entrance to its nest are already partly sprouted; these sprouted seeds are carefully removed from their envelopes and are only carried back into the formicary when thoroughly dry; under such conditions the germ plants are evidently killed. It has been supposed (Moggridge) that the ants allow the seeds to germinate in their nests so the starch will be converted into grape sugar, the whole procedure being somewhat comparable to the malting of grain. Neger, however, discards this explanation because he found that in the sprouted seeds which are placed to dry in the sun the process of germination was not sufficiently advanced to convert any large quantity of starch. He believes, therefore, that the practice of allowing them to sprout has no further purpose than to facilitate the removal of the coatings, which are sometimes very hard to detach from ripe seeds; on sprouted seeds, these envelopes split open and are then easily peeled off by the ants.

Neger has also investigated what happens to the germinated seeds after they have been taken back into the formicaries. He found that, at certain hours of the day, the ants carry out of the nests small, shapeless, pasty masses of a brownish-pink color, which are left to dry in the sun.

When carried out these masses are soft, damp, and bitter to the taste; their size varies from that of the head of a pin to that of a grain of pepper. Microscopic examination shows that they consist of comminuted parts of seeds, plant hairs, fibres, pollen, etc.¹ Neger calls these pasty masses "ant-bread-crumbs" and, although he never saw them being transferred, he supposes that they are eventually carried back into the nest by the ants. In a number of these crumbs he found spores and mycelium of a mould which he identifies with *Aspergillus niger*, having also obtained this fungus in a number of cultures made with fresh "ant-bread-crumbs" taken from worker ants. He formulates the hypothesis that the amylolytic and proteolytic action of this mould may help to render the crumbs more readily digestible so that they can be fed to the young as "larva-bread."

Emery (1912) completely rejects Neger's supposition that the starch and aleurone of the seeds need to be prepared by a ferment before being fed to the larvæ. He offered his colony of *Messor barbarus minor* wheat-paste made up in the form of small rings and found that this substance was readily accepted by the workers, who carried it into the moister part of the nest. There the rings were malaxated for some time and divided into small, twisted pieces, more or less irregular in shape, which were finally dumped into the drier chamber of the nest and never touched again by the ants. Fragments of this paste were also presented by the workers to the larvæ, the largest of which applied their mouth-parts to it just as to other food. Emery determined the weight and starch contents of fifty of these paste rings before and after malaxation by the ants. He infers from his figures that the workers either digested or fed to their larvæ at least 7.3 per cent of the starch and that they consumed also an unknown quantity of nonamylaceous substances, probably proteids; the latter he regards as a much more important aliment than the starch.

This brief consideration of the feeding habits of harvester ants may be properly concluded with Emery's remarks concerning the ethological significance of granivorous behavior among the Formicidæ:

The granivorous ants are derived from insectivorous ants. They represent an adaptation to the climatic conditions of dry prairies, steppes and deserts. When, owing to the summer droughts, insects become scarce and are no longer sufficiently numerous to satisfy the needs of the ants, the granivorous species substitute the living but dried seeds of plants, but at least the species I have observed will not refuse any

¹The composition of these pasty masses suggests great similarity with the pellets found in the infrabuccal pockets of many ants. Part of Neger's "ant-bread-crumbs" may well have consisted of such infrabuccal pellets, which, after being regurgitated by the ants, were merely discarded outside the nest.

insects that may be obtainable. The seeds, however, have the very great advantage that they keep for a long time; they can be accumulated in granaries, thus providing abundant provisions, not exactly for the winter, as the ancient sages maintained, but in general for any periods of scarcity.

Ants and Epiphytes

Wherever in tropical and warm temperate regions the continued dampness of the air allows plants to thrive without being dependent on the soil for their water supply, epiphytes or air plants become an important and often very striking feature of the vegetation. They are especially abundant in the humid rain forest and are at their best in the mountain cloud forests of the tropics. The roots of these plants, boring into the many crevices on the tree's surface and retaining in their network decaying vegetable matter, rapidly loosen the outer layers of the bark and accumulate a cover of humus, affording favorable ecological conditions for a great variety of animals. Ants have not failed to recognize the nesting facilities here offered them by the many nooks and the uniform moisture and ventilation of this aerial root system. Indeed, the botanical collector in the tropics soon learns of the partiality of ants to the cover of humus on tree bark among and beneath the epiphytes.

Though the ethology of the various ants that live with epiphytes has been but little studied, there are a number of observations to show that the interrelations of these organisms are not always merely accidental but have in some cases produced reciprocal adaptation. The reader is referred to the Synopsis of Myrmecophytes (p. 494) for an account of the epiphytic *Myrmecodia*, *Hydnophytum*, and related rubiaceae genera which habitually harbor ants in the tubers of their rhizomes; similar pseudobulbs, inhabited by ants, are also known for a number of epiphytic ferns (p. 497.)

Ridley (1910, pp. 466-470), from observations in Singapore, has called attention to the fact that ants, mainly of the genus *Dolichoderus*, seem to be of considerable importance to the growth of certain epiphytic orchids. As soon as these plants start to grow, the ants bring up soil from the foot of the tree and fill the spaces between the roots, thus constructing shelters in which they raise their brood. This soil supplies nutritive substances to the roots and also keeps them cool and moist. From a comparison with young plants grown under different conditions, it would appear that the presence of ants among the roots is distinctly advantageous to the epiphyte, since seedlings not infested by ants are much weaker and suffer more from the drought. Though certain epiphytes, such as the orchid *Dendrobium crumenatum* Swartz and the ferns

Asplenium nidus Linnaeus and *Platyccerium biforme* Blume, are apparently more attractive than others to ants, Ridley does not mention that any of these plants in Singapore grow only on arboreal ant nests.¹ According to Ule, a number of species of Brazilian ants have acquired the habit of selecting seeds of certain epiphytes, which they carry up trees and shrubs into the crevices on the bark and into the axils of the branches, where they cover them with soil. As the plants grow their entangled roots produce sponge-like ant nests with epiphytic shoots growing out on all sides, the whole resembling "witch-brooms" or bird nests. In certain parts of the Amazonian Rain Forest these aerial agglomerations of plants are so abundant as to form one of the striking features of the scenery. (Ule, 1901, 1905a, 1905d, 1906a, and 1908, pp. 435-436.)

Ule has described two main types of these so-called "ant-gardens." The largest are made by *Camponotus femoratus* (Fabricius) and placed high in the trees of the inundated forest; they consist of the following plants: *Philodendron myrmecophilum* Engler, *Anthurium scolopendrinum* Kunth variety *Poiteauanum* Engler, *Streptocalyx angustifolius* Mez, *Echneca spicata* Martius, *Peperomia nematostachya* Link, *Codonanthe Ulcana* Fritsch, and *Phyllocactus phyllanthus* Link. The smaller gardens are more elegantly constructed and inhabited by species of *Azteca* (*A. traili* Emery, *A. ulei* Forel, and *A. olitrix* Forel); they are preferably placed in the lower trees and show the following flora: *Philodendron myrmecophilum* Engler, *Nidularium myrmecophilum* Engler, *Ficus paraensis* Link, *Marchea formicarum* U. Dammer, *Ectozoma Ulei* U. Dammer, *Codonanthe formicarum* Fritsch, and two Gesneriaceae. Ule claims that, with the exception of *Anthurium scolopendrinum* and *Phyllocactus phyllanthus*, these "ant epiphytes" are so intimately connected with the ants that they are not found in the Amazon Basin in any other station. If Ule's conclusion be true, we have here a most remarkable instance of "selection" practiced by ants. As pointed out by Massart (1906), the results in this case show a striking parallelism with the effects of cultivation by man of crops and vegetables. By persistently caring through countless generations for the cultivated plants, man has gradually deprived them of most of their means of defense in competition with other plants and against the hardships of environment. Crops and vegetables, when left to themselves, are no longer able to hold their own in the

¹Hart (1895) in Trinidad has also noticed the necessity for the presence of ants in the epiphytic clusters of certain orchids in order to assure the healthy growth of these plants. J. Rodway (1911, pp. 132-133 and 139) mentions that, in British Guiana, many of the epiphytic orchids (especially of the genera *Coryanthes*, *Gongora*, and *Oncidium*) shelter large communities of ants in the oval mass of their fibrous roots, the ants filling up the interstices to make a waterproof nest, so that the collector finds it very difficult to dislodge the plant without being severely bitten.

struggle with wild plants. Similarly, in the case of the plants domesticated by the ants in their "gardens," though it is certain that the seeds of these epiphytes are occasionally dropped elsewhere in the forest, they have lost the devices which allowed them to fight their rivals and are at present doomed unless cared for by the ants.

The partiality of certain ants to the clusters of *Tillandsia* and other epiphytic bromeliads was first noted by Wheeler (1901a, pp. 526-528, and 1901b) in Mexico. He relates his experiences as follows:

On accidentally pulling to pieces one of the large bud-like epiphytic tillandsias (probably *Tillandsia Benthamiana* Klotzsch), very common both in this and other localities about Cuernavaca, I was surprised to find it containing whole nests of ants, with their larvae and pupae snugly packed away like so many anchovies in the spaces between the moist overlapping leaves. A closer inspection showed that the ants had gnawed little holes through the leaves to serve as entrances to their chambers. These holes occasionally perforated a single leaf, but quite as often they threaded several leaves and extended to the very core of the bud. Sometimes a single colony of ants was divided up into companies, each occupying the space under a single leaf. But the most remarkable fact concerning these nests was the frequent occurrence of two or even three flourishing colonies belonging to different species in a single tillandsia, the whole habitable basal portion of which was rarely more than two to three inches long by one and one-half inches in diameter. Often these colonies were curiously intermingled in such a manner that there was no actual blending and the space under a single leaf was always occupied by ants of the same species, still, whole colonies or portions of a single colony were often completely surrounded by leaf spaces occupied by another colony.

Wheeler collected the following ants from these Mexican tillandsias: *Pseudomyrma gracilis* (Fabricius) variety *mexicana* Emery, *Crematogaster brevispinosa* (Mayr) variety *minutior* (Forel), *Leptothorax petiolatus* Forel, *Cryptocerus aztecus* Forel, *C. wheeleri* Forel, *Camponotus rectangularis* Emery variety *rubroniger* Forel, and *C. abdominalis* F. Smith variety. Though the tillandsias appear to suffer no injury from their tenants, Wheeler is not inclined to regard this association of plants and ants as a case of symbiosis, because at least four of the seven species enumerated above occur also under other conditions in the neighborhood of Cuernavaca.

Wasmann (1905a, p. 210, Pl. VII, fig. 1) also describes and figures an interesting carton nest of *Crematogaster sulcata* (Mayr), from Rio Grande do Sul, Brazil, which was interwoven in a pensile cluster of epiphytic tillandsias. Calvert (1911), in Costa Rica, found the clumps of epiphytic bromeliads frequently inhabited by ants, especially by the large black species *Odontomachus hastatus* (Fabricius) "with enormously developed jaws, bent near the tip, which are carried wide open and measure one-quarter inch from tip to tip; occasionally they would be

snapped shut with a very audible click."¹ A species of *Apterosigma*, one of the fungus-growing ants, was also found on one occasion by Calvert in a clump of Costa Rican bromeliads.²

A curious case of parabiosis between *Odontomachus affinis* Guerin subspecies *mayi* Mann and *Dolichoderus debilis* Emery variety *rufescens* Mann was observed by Mann (1912, pp. 36-41) in Matto Grosso, Brazil. These two species of ants were nesting together in an earthy structure built in the fork of the branches of a tree about 40 feet above the ground: "Five roots of a plant ramified through this nest in all directions in such a manner as to make it quite firm, despite the nature of its component material." As noted by Wheeler, this nest was really an "ant-garden" of the type described by Ule.

Quite recently Wheeler (1921) has published much additional information with regard to similar "ant-gardens" or "flower-gardens" which he found common in the forest and jungle near the Tropical Research Laboratory of the New York Zoological Society at Kartabo, British Guiana. These gardens agreed very closely with Ule's description even in their floral make-up. Among the plants growing out of the spherical or elliptical lumps of black earth, which vary from the size of a walnut or orange to that of a foot-ball, two Gesneriaceae (probably species of *Streptocalyx* and *Codonanthe*), an *Anthurium*, a *Peperomia*, and a few bromeliads were recognized. In British Guiana four different ants establish flourishing colonies in the gardens, namely, *Camponotus* (*Myrmotherix*) *femoratus* (Fabricius), *Crematogaster limata* F. Smith subspecies *parabiotica* Forel, *Anochetus* (*Stenomyrmex*) *emarginatus* (Fabricius), and one or more small, black species of *Azteca* very closely related to, if not the same as, the species taken by Ule in Brazil. The *Camponotus* and *Crematogaster* are by far the most frequent, occurring in fully 90 per cent of the gardens; the *Aztecæ* are rather sporadic and the *Anochetus* even less numerous. In more than 80 per cent of the gardens *Camponotus* and *Crematogaster* nest together in friendly parabiosis. The former, large and aggressive, and the latter, tiny and timid, mingle in the same long files that continually ascend and descend the trees, traverse the soil and explore the foliage. Their main occupation is to herd the

¹According to Mjöberg, another ponerine, *Myrmecia mjobergi* Forel, of the dense Rain Forest of Queensland, builds its nest high on the trees in the clusters of epiphytic *Platyserium*. It is stung much dreaded by the natives (Forel, 1915, *Arkiv. f. Zool.*, IX, No. 16, p. 7).

²Picado, in a recent paper on the fauna of Costa Rican bromeliads (1913, p. 273), evidently has misunderstood Calvert, for he writes: "Parmi les animaux broméliocoles mycophages, on peut citer quelques espèces de Fourmis du genre *Odontomachus*, dont la nourriture habituelle est constituée par des Champignons." *Odontomachus* is a ponerine ant not known to feed on fungi. Picado also speaks of finding several species of ants in epiphytic clusters of Bromeliaceae (*op. cit.*, p. 348), but only mentions by name those indicated by Calvert.

jassids and membracids and collect the secretion of extrafloral nectaries. Examination of such "compound nests" revealed that all the superficial galleries, and they alone, are stuffed with *Crematogaster* and their brood, whereas only the center, or core, of the garden is occupied by the *Camponotus* with their larvæ and cocoons. The galleries of both species, however, open into one another so that the adult ants undoubtedly move about together more or less.

The conclusions drawn by Wheeler from his observations differ in several important particulars from Ule's. The frequent parabiosis of *Crematogaster* and *Camponotus* shows that Ule's distinction of gardens on the basis of the size of the ants inhabiting them does not hold in British Guiana. Moreover, though the same plants do not occur in all gardens, no preference of certain ants for certain plants could be detected. All the species of ants found in the ant-garden biocenose may also nest elsewhere, but it must be admitted that *Camponotus femoratus* shows a decided preference for the garden nest, so that we have here a very regular and intimate ethological relationship between an ant and certain epiphytes. According to Wheeler the ant-gardens are not started in the manner implied by Ule, viz., by means of the ants either putting seeds into crevices or accumulating a certain amount of humus at some spot on a tree or bush and then collecting and planting the seeds in the mass. It is more probable that the young ant epiphytes originally grow in small accumulations of earth or detritus, which are ultimately settled by colonies of the ants. That the amount of humus is gradually increased by the ants with the growth of the colony admits of no doubt, and it is possible that as the accumulation becomes greater, it may be sown with seeds falling from the original plant. Furthermore, it is practically certain, from what we know of the habits of ants, that new gardens cannot be seeded from old ones, as Ule maintains, for this would be too great a task for the single fecundated queens which start the new colonies. Ule's experiments with ants transporting the seeds of these epiphytes do not furnish conclusive proof that the insects actually sow the plants, for ants will often carry all sort of portable organic bodies into their nests, only to cast them out later when they find them useless. And lastly, Ule records no convincing observations in support of his contentions that the ants actually cultivate the growing plants. Wheeler believes, therefore, that it is advisable to suspend judgment for the time being as to the provenience and significance of the plant elements in the ant-garden biocenose of tropical America.

The association of ants with certain species of *Dischidia*, a genus of epiphytic Aselepiadaceæ in the Oriental Region, has been treated in detail in a preceding chapter (p. 357) and other aspects of it are considered in the sequel (p. 520).

Gall-inhabiting Ants

The habit of sheltering their brood within old galls produced by various insects is very common with ants and is worthy of careful study for several reasons. In the first place, certain species of ants are so frequently found in galls that this location of their nests has become part of their normal behavior. Secondly, most galls have such regular shape and structure that often they look like normal productions of the plant; when settled by ants they may then simulate true myrmecodomatia and become a source of confusion in the study of myrmecophytism. Thirdly, the gall-inhabiting behavior of ants can help us to understand the origin and meaning of myrmecophily proper in plants. And, finally, as shown by Prof. Bailey's histological studies, certain myrmecodomatia occupy a somewhat intermediate position between normal plant structures and galls, since the intervention of the ants results in the production of hyperplasias or abnormal tissues by the plant.

Gall-inhabiting ants are rarely met with in the colder regions of the globe, where the rigor of winter prevents these insects from acquiring true arboreal or epiphytic nesting habits. Patton (1879), however, recorded finding in Connecticut, nests of *Leptothorax curvispinosus* Mayr (= *Stenammina gallarum* Patton), with queen, workers, and larvæ, in deserted, dead galls of *Gelechia gallæsolidaginis* Riley on the stems of goldenrod (*Solidago* species) and in those of *Cynips spongifica* Osten Sacken on oaks; and H. Ross (1909) has mentioned the frequent occurrence in southern Germany of *Crematogaster brevispinosa* Mayr variety *minutior* Forel in old oak-galls.

On the other hand, the gall-inhabiting behavior becomes part of the normal habits of many species of ants in the xerophytic and warmer parts of the southern Neartic and Palearctic Regions. Wheeler (1904a, pp. 155-158; and 1910b, pp. 208-212) has written a most entertaining account of the ant-fauna of the spherical, woody galls produced by the cynipid *Holcaspis cinerosus* Bassett on the twigs of the Texan live oak. *Crematogaster lincolata* (Say) subspecies *lacinsecula* Mayr and its variety *clara* Mayr merely use them as temporary shelters for the workers, but *Leptothorax obturator* Wheeler, *L. fortinodis* Mayr, *Camponotus caryæ* (Fitch) variety *decipiens* Emery and its subspecies *rasilis* Wheeler.

and *Colobopsis abdita* Forel variety *etiolatus* Wheeler are able to bring their males and virgin females, as well as numerous workers, to maturity within the narrow confines of these galls. Nevertheless, all of these species may also be found nesting in dead wood. The *Colobopsis* is particularly interesting because of the peculiar shape of the head which, in the major workers, is truncated in front; with this flattened, anterior part, the soldiers block the entrance to the nest, stepping aside only at a tactile signal given by an incoming worker. In Sicily, De Stefani-Perez (1905) commonly found colonies of *Crematogaster scutellaris* (Olivier) and *Leptothorax tuberosum* (Fabricius) inside old, deserted galls of *Cynips toza* Bosc; and others of *Leptothorax nylanderii* (Forster) in empty galls of *Cynips kollari* Hartig.

Having paid special attention to plant galls during my sojourn in the Belgian Congo, I frequently found ants nesting inside such deserted structures. While this was rather common in the drier, open Savannah country, I cannot at present recall a single instance of a gall-inhabiting ant in the Rain Forest. This is probably due to the fact that the great majority of galls in the moist, forested areas are produced by soft-tissued organs, such as leaves, flowers, and the like, which drop off and decay soon after being left by their makers. In the Savannah woody galls are much more frequent; these, when empty, remain for many months or even years on bush or tree, their solid walls enclosing ideal shelters for ant colonies.

The following are a few of the ants which I found nesting in deserted galls in Katanga, during the years 1911 and 1912.

Cataulacus luteus Forel variety *gilviventris* Forel and *C. bequaerti* Forel were found at Kabanza, near Kikondja, nesting in empty lepidopterous galls on a tree.

Leptothorax innocens Forel had established regular fornicaries, with larvae and pupae, inside an old gall of a tree at Elisabethville.

Crematogaster gallicola Forel and its various forms seem to be common gall-inhabiting ants throughout the range of the species. The typical form was originally found by Liengue at Delagoa Bay, "in einer Stengelgalle" (Forel, 1894, p. 95), and Arnold (1920, p. 533) found a colony of it, with queen and workers, in a gall at Somabula, Southern Rhodesia. The subspecies *latro* Forel was described from the Kalahari, where, according to L. Schultze, it lives "in gallenartigen Anschwellungen der Zweige einer Akazie mit Blattläusen." I collected the subspecies *spuria* Forel, with larvae and pupae, from old twig galls on *Mouotes katangensis* É. De Wildeman at Elisabethville; while the variety *oraclum* Forel¹ was very common at Sankisia in a cecidium on the branches of *Dalbergia Bequaerti* É. De Wildeman.

To the foregoing could be added for Africa:

¹According to Arnold, this form should be named *Crematogaster bulawayensis* (Forel).

Tapinoma arnoldi Forel builds its small nests within hollow galls in Southern Rhodesia (Arnold, 1915, p. 155).

Cataulacus rugosus (Forel) was originally described from Delagoa Bay, where Lieugne found it in empty caulinary galls (Forel, 1894, p. 78).

Crematogaster castanea subspecies *ferruginea* variety *durbaensis* (Forel) makes its nests in Southern Rhodesia "in hollows in trees, or in hollow branches, and more rarely in galls; elsewhere it has been recorded as making large carton nests, attached to the branches of trees and shrubs" (Arnold, 1920, p. 493).

Polyrhachis cubaensis subspecies *gallicola* Forel was described from specimens found in galls at Delagoa (Forel, 1894, p. 71).

The coccid *Houardia troglodytes* Marchal was found in populous colonies, together with a species of *Crematogaster* (allied to *C. kneri*), occupying spacious cavities in the branches of *Balanites aegyptiaca* Delile in Senegambia. Since the branches had swellings corresponding to these cavities, it would seem that the ants had taken possession of empty galls, bringing the scale insects with them (P. Marchal, 1909a, p. 586; 1909b, pp. 171-173).

At Leopoldville, in May 1915, I was much puzzled over certain swellings inhabited by *Crematogaster depressa* (Latreille) variety *fuscipennis* Emery on the branches of a small rubiaceaceous shrub, and for some time I was in doubt as to whether they were true myrmecodomatia. Subsequent examination of some of these swellings on younger branches showed that they were galls produced by a caterpillar. I have already pointed out that it is by no means always easy to distinguish between insect galls and myrmecodomatia, and the origin of ant-inhabited swellings or pouches of unknown plants should therefore be studied with the utmost care. Galls have, in fact, been described as myrmecodomatia and the plants on which they were found erroneously regarded as myrmecophytes. The two following examples are taken from the African flora; but a similar confusion has been made elsewhere, too, as, for instance, in the case of the Indian *Ficus inaequalis* described and figured by Schimper as a myrmecophyte (Ridley, 1910, p. 458). It is possible that similar errors have found their way into the general synopsis of myrmecophytes given in the sequel.

Clerodendron formicarum Guerke¹ (= *C. Lujæ* E. De Wildeman and Th. Durand) is not, as its name would imply, a myrmecophilous plant. It is found rather commonly in the open grass-country north and south of the Congo forest: in the Lower Congo, Kasai, Katanga, and northeastern Uele. I frequently observed it in Katanga (1911) and found that practically all specimens show one or more spheroidal or pear-shaped swellings, 7 to 15 mm. in diameter, on the stem, the petiole, or the flower

¹Described in Engler's Bot. Jahrb., XVIII, 1894, p. 179. A good illustration is given by Thonner, 1908, 'Die Blütenpflanzen Afrikas,' Pl. cxxxiv; fig. C of this plate represents the galls as "Blätter mit von Ameisen bewohnten Anschwellungen."

stalk. Often the swelling is symmetrically developed, especially when occurring on a petiole, but in many cases it bulges more on one side of the support. Two galls may be placed close, one above the other, or even partly united. A cross-section of a young swelling shows the typical structure of a pith gall: a spacious central cavity, completely closed and surrounded by the hypertrophied fibrovascular tissues of the stem. In young galls I always found a single larva of a lace-bug belonging to the genus *Copium* (Tingitidæ) feeding inside the cavity on the pith cells along the wall. When the *Copium* reaches the adult stage, the "ripe" gall splits open, allowing the bug to escape. Such old, empty galls may eventually be invaded by ants, but I have never observed this myself. I am, therefore, fully satisfied that the swellings of *Clerodendron formicarum* are true insect galls. That they are not real myrmecodomatia is moreover indicated by their irregular distribution over various parts of the plant.¹

We now come to a consideration of the so-called myrmecophilous acacias of Tropical Africa. These plants present a rather difficult problem, and, though I myself am convinced that they are not true myrmecophytes, the facts in the case are still far from being satisfactorily elucidated. Unfortunately, I have never had an opportunity to study them in the field.

While travelling across the deserts of Nubia and Sennaar in 1867, G. Schweinfurth discovered a curious, shrubby *Acacia*, which he described and figured under the name *Acacia fistula* (1867, p. 344, Pls. IX and XIII). Some of the thorns of this plant were considerably swollen, hollowed out, and pierced by an orifice; the wind playing on these empty swellings produced a whistling noise, the plant being therefore called "Ssoffar," or flute, by the natives. Schweinfurth did not record the occurrence of ants in the swellings² but stated that the small, circular orifice was pierced "by the escaping insect," the swellings being, in his opinion, true insect galls, a view endorsed by Ascherson (1878, p. 44).

Many travellers have since remarked upon the abnormally swollen thorns of certain East African acacias and have also called attention to the fact that they are frequently settled by ants. According to Harms' recent account³ the following African species of the genus *Acacia* have been found with ant-inhabited swellings:

¹Various species of *Copium* produce galls on several Central African *Clerodendrons*; they most frequently affect the flowers. *Copium atolidum* Horvath, for instance, very commonly deforms the flowers of *Clerodendron spinescens* Guerke.

²Keller (1892 a, p. 137), however, asserts that Schweinfurth found ants inside the swollen thorns of this *Acacia fistula*, though he did not mention the fact in his paper.

³In Engler, 1915, 'Die Pflanzenwelt Afrikas,' III, 1, pp. 368-373; see also Harms, 1914, Engler's Bot. Jahrb., LI, pp. 361-365.

Acacia fistula Schweinfurth and *A. zanzibarica* (Sp. Moore). In Harms' opinion these two forms are hardly specifically distinct from the common African *A. seyal* Delile.

A. drepanolobium Harms.

A. formicarum Harms. This is probably Sjöstedt's "Flotenakazie" from the Masai-steppe.

A. pseudofistula Harms.

A. malacocephala Harms.

A. Bussei Harms.

The exact nature of the swollen thorns of these plants has been somewhat disputed. As mentioned before, Schweinfurth and Ascherson regarded them as true galls. This opinion is further supported by the thorough researches of Keller (1892a) and Sjöstedt (1908), as well as by the more recent observations of Glover Allen (Wheeler, 1913, p. 130, footnote), H. Winkler (1912, p. 65), and H. Schenck (1914, p. 453). Sjöstedt was unable to discover the maker of the galls; yet he believes that they may owe their development to the sting of some dipterous or hymenopterous insect. Glover Allen, however, found that the enlarged thorns of *Acacia fistula* (from the Nilotic Sudan) consist, when young, "of a solid mass of green, succulent tissue, with a single small larva inside, as in a typical insect gall"; and H. Winkler discovered in German East Africa a beetle-larva in a swollen *Acacia* thorn that was entirely intact. Alluaud and Jeannel are, it seems, the only observers inclined to believe that the ants themselves produce the galls,¹ but their own observations hardly support this view.

During his travels in British East Africa with R. Tjäder, in 1906, Mr. H. Lang made some observations on gall-bearing acacias growing in large numbers on the Athi Plains. One of his photographs of these curious plant deformations is reproduced on Plate XXVI, fig. 2. From information he kindly gave me, I am led to agree with Sjöstedt and others that the swellings are true insect galls.² They are not found on all specimens of the same species of *Acacia*, even in one locality: while on some plants practically all the thorns are swollen, others nearby bear hardly any galls; furthermore, their size is quite variable and their shape rather irregular. Mention may still be made of the fact that,

¹ "En somme, nous ne pouvons pas affirmer avec certitude quels sont les rapports exacts du *Crematogaster vulcania* avec l'*Acacia* sur lequel on le trouve, mais ce que nous avons vu nous pousse fortement à croire que ce sont bien les *Crematogaster* qui provoquent par leur intervention à l'extrémité des rameaux jeunes, la formation des galles, qui entretiennent leur accroissement, puis le moment venu les perforent pour y installer leur nid" (Santschi, 1911, p. 100).

² Some authors admit that the swellings of the thorns of African acacias are not due to ants, yet call them ant-galls (" Ameisengallen"). This misleading term should be avoided, because it conveys the erroneous idea that the ants are responsible for the production of the galls. Even the myrmecodomatia of true myrmecophytes are normally produced by the plant without the intervention of ants; though, when inhabited by these insects, some tissues in certain species may show a peculiar hyperplasia.

while the species of *Acacia* enumerated above have a rather wide distribution in eastern Central Africa, swollen thorns have been noted in only a few localities within their range.

The conclusion thus seems plainly justified that these East African acacias should be excluded from the list of true myrmecophytes. Sjostedt still clings to the idea of a mutualistic symbiosis between these plants and the ants which often settle their hypertrophied thorns. In case the swellings are typical insect galls, I do not see how this view can be supported by facts. The excellent nesting sites offered by old acacia galls are merely exploited by the ants, and it is doubtful whether the plant derives any benefit from the presence of these insects; certainly, the galls must be considered as pathological productions, which could hardly be of utility to the economy of the plant. Moreover, as pointed out by Wheeler, it is by no means clear that the acacias are not sufficiently protected by their long, sharp thorns from browsing animals.¹

The following ants have been found inside thorn galls of African acacias:

Crematogaster brunneiyeunisi subspecies *acaciae* (Forel), in thorn galls of *Acacia fistula*, Abyssinia (Keller, 1892a).

Crematogaster chiarinii Emery, in thorn galls of *Acacia zanzibarica*, near Kahe, in the plain at the foot of Mt. Kilimanjaro (Sjostedt, 1908); and its variety *cineta* Emery, in swollen thorns of *Acacia fistula*, Somaliland (Keller, 1892a), together with *Pausus spicicola* Wasmann (Wasmann, 1892 and 1915).

Crematogaster gerstaeckeri (Dalla Torre) (= *C. cephalotes* Gerstaecker), in a thorn gall of *Acacia* near Mombasa (Gerstaecker, 1871, p. 356).

Crematogaster ruspolii Forel, in thorn galls of *Acacia fistula*, Abyssinia (Keller 1892a).

Crematogaster sjostedti (Mayr), in thorn galls of *Acacia drepanolobium*, near Kahe, in the plain at the foot of Mt. Kilimanjaro, and in West Usambara (Sjostedt, 1908).

Crematogaster nigriceps subspecies *prelli* (Forel), taken by Prell from thorns of "*Acacia cornigera*" in the plain of Kahe, German East Africa.

Crematogaster castanea F. Smith (= *C. tricolor* Gerstaecker), in thorn galls of an unidentified *Acacia* of the Masai steppe, probably *A. formicarum* (Sjostedt, 1908).

Crematogaster rivai Emery, described from swollen spines of *Acacia larin*, Abyssinia (Emery, 1897, p. 600).

Crematogaster nigriceps Emery was found by Ituspoli in swollen spines of *Acacia larin* in Somaliland (Emery, 1897, p. 601).

Crematogaster mimosa (Santschi) was found by C. Alluaud in thorn galls of *Acacia stenocarpa* on Mt. Kenia at about 2000 m. (Santschi, 1914, p. 89).

Crematogaster vulcania (Santschi) was collected by Alluaud and Jeannel from swollen thorns of an acacia (*Acacia stenocarpa*?) in the steppe of the Rift Valley, at the foot of Mt. Longonot (Santschi, 1914, pp. 96-98).

¹The Central and South American bull-horn acacias are true myrmecophytes. A resume of the observations made on these remarkable plants is given in the synopsis of myrmecophytes (pp. 510).

Crematogaster (Decacrema) solenopsides subspecies *flavida* (Mayr), in thorn galls of *Acacia Bussei*, Usambara (Sjostedt, 1908); the variety *gallarum* (Santsehi) was taken in galls of an acacia at Mindouli, French Congo.

Cataulacus intrudens (F. Smith), in thorn galls of *Acacia Bussei*, Usambara (Sjostedt, 1908); originally described from thorns of *Acacia*, in Natal.

Tetraponera penzigi (Mayr), in thorn galls of *Acacia drepanolobium*, near Kahe, in the plain at the foot of Mt. Kilimanjaro, and in West Usambara (Sjostedt, 1908).

Tetraponera natalensis F. Smith was taken from thorns of a species of *Acacia* in Natal (F. Smith, 1876).

According to Kohl (1909, p. 151), H. Schinz found ants inside hypertrophied thorns of *Acacia horrida* in South Africa.

As would be expected from the fortuitous production of galls on plants, none of the ants mentioned in the preceding pages seems to restrict the location of its nest to galls. They are evidently all arboreal species which are in the habit of sheltering their brood in hollow branches or cavities of trees.

Fungus-growing Ants

Allusion has been made above to the depredations of the South American leaf-cutting, or parasol, ants. Though the destruction wrought by these insects was familiar to the indigenes and early colonists, what use is made of the vegetable matter carried into their nests is a discovery of comparatively recent date. H. W. Bates in his classical 'Naturalist on the Amazon' (1863, I, pp. 23-26) describes the activities and earth-works of the large South American leaf-cutter, *Atta cephalotes* (Linnaeus), in great detail. In his opinion, "the leaves are used to thatch the domes which cover the entrances to their subterranean dwellings, thereby protecting from the deluging rains the young broods in the nest beneath." Lincecum (1867), Norton (1868), and B. R. Townsend (1870), who studied the smaller Mexican and Texan parasol ants, all overlooked the most important peculiarity in the behavior of these insects.

Belt (1874) was the first to understand the true significance of the leaf-gathering habit. He definitely states that the parasol ants use the leaves "as a manure, on which grows a minute species of fungus, on which they feed;—that they are, in reality, mushroom growers and eaters." He then proceeds to describe the interior of the nests of the species of *Atta* studied by him in Nicaragua.

The chambers were always about three parts filled with a speckled, brown, flocculent, spongy-looking mass of a light and loosely connected substance. Throughout these masses were numerous ants belonging to the smallest division of the workers, which do not engage in leaf-carrying. Along with them were pupae and larvae, not gathered together, but dispersed, apparently irregularly, throughout the flocculent

mass. This mass, which I have called the ant-food, proved, on examination, to be composed of minutely subdivided pieces of leaves, withered to a brown color, and overgrown and lightly connected by a minute white fungus that ramified in every direction throughout it. I not only found this fungus in every chamber I opened, but also in the chambers of the nest of a distinct species that generally comes out only in the night-times. When a nest is disturbed, and the masses of ant-food are spread about, the ants show great concern to carry away every morsel of it under shelter again.

Belt's observations were subsequently confirmed by Fritz Müller (1874), Tanner (1892), A. Møller (1893), Sampaio (1894), H. v. Ihering (1894 and 1898), Urich (1895a-b), Swingle (1896), Forel (1896a-c, 1897), Wheeler (1901b, 1905b-c, 1907, 1910b, etc.), Gældi (1905a-b), J. Huber (1905, 1907, 1908), and others. It is now an established fact that the Attini, a tribe of myrmicine ants restricted to America, are all intimately associated with fungi, which they cultivate on an appropriate substratum and which in turn supply these insects with their only food.¹ They are the only ants known to be strictly vegetarian. Various stages in the development of the fungus-growing behavior may still be recognized among the many forms of the tribe.² The different members of the lower genus, *Cyphomyrmex*, and probably also of *Myrmicocrypta*, make a small, crude nest; they collect caterpillar excrement on which they grow a floeculent mycelium with well-developed food-bodies, or bromatia (called "kohlrabi-heads" by A. Møller); their gardens are only a few centimeters in diameter, of irregular shape, and lie on the floors of small dilations in the rough earthen galleries of the nest. *Apterostigma*, *Sericomyrmex*, *Mycetosoritis*, and *Trachymyrmex* all excavate more regular nests and construct pendent mushroom gardens on a substratum of insect excrement and vegetable debris. The gardens of *Apterostigma* are sometimes provided with a special mycelial envelop, but those of all other Attini are naked. *Mallerius* and *Acromyrmex* make one or more large gardens on the floors of the nest-chamber. And, finally, the *Attæ*, s. str., which include the true parasol ants, the largest and most powerful species of the tribe, collect large quantities of leaves, flowers, and other vegetable substances for their gardens; their nests attain huge dimensions and comprise a number of large chambers, each with a sessile mushroom garden of triturated plant fragments, permeated with fungus hyphæ.

¹The genus *Proatta*, recently discovered by v. Buttel-Reepen in Sumatra, was originally placed by Forel among the Attini, but later separated by the same author to form a tribe of its own. There is nothing to show that this Sumatran ant has developed fungus-growing habits.

²The habits of the genus *Blepharidatta* Wheeler are unknown.

The origin of new colonies among the Attini and the method of transferring fungus culture from the maternal to the daughter colony have been investigated by H. v. Ihering (1898), Gældi (1905a), and J. Huber (1905, 1907, and 1908). The dealated, fertilized female of *Atta sexdens* (Linnaeus) often starts a new colony alone; she digs a burrow in the soil and forms at a depth of 20 to 30 cm. a chamber in which she deposits within a few days a little packet of eggs. Even at that time one finds beside the eggs a flat heap of loose white substance, only 1 to 2 mm. in diameter, which is the earliest rudiment of the fungus garden. On searching for the origin of the fungus germs with which this new garden is established, v. Ihering discovered that every *Atta* queen, on leaving the parental nest, carries in her infrabuccal pocket a loose pellet of debris containing also hyphæ from the fungus gardens. This fact was confirmed by J. Huber, who successfully reared an *Atta* colony from its inception to the appearance of the first workers. The day following the nuptial flight the female disgorges this pellet on the floor of the newly dug chamber; to keep the fungus alive she frequently manures parts of it with liquid excrement from the tip of her gaster. In this early stage of the colony the queen does not feed on the fungus but eats a great number of her own eggs. The first larvæ, too, are fed directly on eggs thrust into their mouths by their mother. Shortly after hatching, the first workers usurp the functions of the mother ant, which henceforth degenerates into an egg-laying machine. They manure the garden with fecal droplets and feed the larvæ with their mother's eggs, while they themselves feed on the bromatia meanwhile developed on the hyphæ. A few days later the workers start to extend the formicary; they also break through the surface of the soil and return with new material for the fungus garden. In the meantime, the bromatia have become so abundant that they can be fed to the larvæ. Huber also observed that the founding of a new colony by a queen is often unnecessary, because fertile females of *Atta sexdens* are readily adopted by strange workers of their own species, thus adding to the strength of existing formicaries.

The systematic position of the fungi grown by the Attini is still disputed. A. Møller is apparently the only botanist to have made a special point of studying this problem. His attempts, however, to raise any fruiting form from mycelial cultures started with portions of the fungus gardens of ants were unsuccessful. But he found in four instances an agaricine mushroom, which he called *Rozites gongylophora*, growing on extinct or abandoned *Acromyrmex* nests. From the basidiospores of this plant he succeeded in raising a mycelium resembling in all respects that of

the ant-gardens. Three of the species of *Acromyrmex* did not hesitate to eat portions of this mycelium and also of the pileus and stem of the *Rozites*. Moller therefore identified the fungus grown by *Acromyrmex* with his *Rozites gongylophora* and in this he has been followed by most other investigators. Wheeler (1910^b, pp. 327-328), however, maintains that Moller's observations are far from conclusive. He believes that the fungi cultivated by the ants may be more closely related to the moulds (Ascomycetes) than to the toadstools (Basidiomycetes). He has even described the peculiar fungus grown by the Texan *Cyphomyrmex rimosus* (Spinola) variety *comalensis* Wheeler as *Tyridiomyces formicarium*, assigning it provisionally to the Exoascaceae (Wheeler, 1907, p. 772).¹

There can be little doubt that the highly specialized fungus-growing behavior of the Attini must have been gradually derived from some more primitive fungus-eating habit. How this developed is at present a matter of conjecture, but it may be expected that other ants will show vestigial fungicolous habits. When these have been properly studied, they may, taken in addition with what is known of the ethology of other fungus-growing insects, give us a proper clue to the possible evolution of the complicated ethology of the Attini.

A condition very near the primitive fungus-growing behavior is perhaps exemplified in the remarkable carton nests of the European *Lasius fuliginosus* (Latreille). I quote the following description from Donisthorpe's recent volume on 'British Ants' (1915, p. 193):²

These nests are often very large, having the appearance of a huge sponge, and consist of a number of irregular cells separated from each other by thin carton walls, which are rather brittle and generally black in color, but sometimes light brown, according to the amount and the color of the earth used in their construction. The carton contains a quantity of a fungus which was named *Septosporium myrmecophilum* by Fresenius (1852, p. 49, Pl. vi, figs. 29-31). Saccardo (1886, p. 538) describes it as *Macrosporium myrmecophilum* but considered it might be identical with *Cladotrichum*, and Lagerheim (1900) came to the conclusion that it was really a *Cladotrichum*, and called it *C. myrmecophilum*. I supplied Dr. Jessie Baylis Elliot of the Birmingham

¹Spegazzini has also given descriptions of fungi taken from the gardens of various Attini in Argentina. He regards *Beruelinia I. belti* Spegazzini (1899, p. 311) as one of the Discomycetes. *Rhizomorpha formicarium* Spegazzini (1899, p. 352) is probably the sterile form of one of the Xylariaceae. Both these fungi were found in the mushroom gardens of *Acromyrmex lundii* (Guerin). *Monilia formicarium* Spegazzini (1910, p. 414), described from the nests of *Atta hystrix*, is one of the many imperfect fungi of unknown affinities. Prof. Wheeler has kindly sent to me for publication the following extract from a letter written by Mr. Carlos Bruch, dated La Plata, Argentina, July 16, 1921: "You will, no doubt, be interested in the discovery of the mushrooms which are cultivated by some of the Argentinian Attini. *Acromyrmex lundii* cultivates *Xylaria micrura* Spegazzini; *A. (Maüerius) hegeri*, *Poroniopsis bruchi* Spegazzini; and *Atta wollenweideri* a gigantic agaricus, *Locetina mazzuchii* Spegazzini. This year I found on the culture substratum that had been carried out into their hills by the ants hundreds of *Poroniopsis* in every nest. Masses of substratum which I had sifted for guests two months previously were completely covered by the mushrooms. The damp autumn months this year were particularly favorable to the development of the mushrooms mentioned." *Xylaria* and *Poroniopsis* are both Pyrenomycetines (Ascomycetes) of the family Xylariaceae; *Locetina* is one of the Hymenomycetines (Basidiomycetes) and placed in the family Agaricaceae. *Rozites* is also a genus of the Hymenomycetines.

²I have inserted in parenthesis the dates and pages of the references.

University with various samples of *D. fuliginosa* carton, and she has proved, by making cultures, etc., that the fungus it contains is a *Cladosporium*, and so should be called *Cladosporium myrmecophilum* (J. B. Elliot, 1915, p. 138, Pl. VIII, figs. 1-4). The "raison d'être" of this fungus is probably twofold; the hyphae may act as food for the ants and their brood—it forms a delicate bluish mould on the walls of the cells and under the microscope it may be seen to have been bitten off by the ants—and the mycelium helps to strengthen the walls of the nest. The ants most probably cultivate this fungus intentionally, as no other species of fungus is found in these nests, but it would not alone supply sufficient food for the teeming myriads that form the population of a large colony.

No definite proof has apparently been given that the fungus in the carton nest of *Lasius fuliginosus* contributes to the diet of the ants, but Donisthorpe remarks that "the great difficulty experienced in rearing *fuliginosa* larvae in captivity—when no carton is present—would seem to show that the fungus is necessary as food, though the ants feed on other substances as well." Adlerz (1913, p. 63) and Donisthorpe (1915, p. 229) have shown that *Lasius umbratus* (Nylander) also builds carton nests with inner walls covered by the hyphae of a fungus. Dr. J. B. Elliot (1915, pp. 139 and 142, Pl. II, figs. 5-10) described the hyphae found in one of these nests in England as a variety *myrmecophilum* of *Hormiscium pithyophilum* (Wallrich), a fungus which is usually found in thick, superficial patches of mycelium on the leaves of pines, firs, and yews.¹

According to Dr. J. B. Elliott (1915, p. 142), the species of fungus associated with the carton of *Lasius fuliginosus* is always the same, which also holds true in the case of *L. umbratus*. "Since the fungus exists in the carton as a pure culture, all 'foreign' fungi are doubtless 'weeded' out, as in the fungus gardens of the white ants and the leaf-cutting ants, for many varieties of fungus spores must be introduced into the nests by the passing of insects in and out."

It seems likely that certain, at least, of the many tropical ants which construct nests either of carton or of more loosely agglutinated plant-fibres, will eventually show similar associations with fungi. Farquharson (1914), in Southern Nigeria, several times found fungous hyphae growing on the aerial shelters composed of chewed wood and built over coccids by a species of *Crematogaster*. But it is very doubtful whether the ants had anything to do with this fungus. Perkins suggested that the mycelium in this case may merely have grown on the excreta of the coccids or even on the scale insects themselves. The roughly woven

¹These fungi from the nests of *Lasius fuliginosus* and *L. umbratus* are all conidia-bearing or sterile mycelia of uncertain systematic position.

nests of the African *Macromischoides aculeatus* (Mayr) are frequent on leaves in the forest. They have been described by Santschi as lined with a mycelium bearing fructifications. Prof. Wheeler's examination of nests of this species (p. 190) argues for the probability that this fungus has no relation with the ants, being but one of the many fungi which in the moist tropical forest grow over dead vegetable matter. *Chromosporium formicarum* Ferdinandsen and Winge (1908, p. 21, Pl. II, fig. 11) is another imperfect fungus found by Raunkiaer on the island of St. John, West Indies. Its brown-yellow conidia covered the walls of galleries in a decaying log occupied by unidentified ants. The writers assume that the ants feed on these conidia, but this will need actual confirmation.

A few words may be said about the peculiar fungi found growing on the inner walls of the myrmecodomatia of certain ant-plants. Mische (1911b, pp. 331-341) made the interesting discovery that some of the galleries in the pseudobulbs of the Javanese *Myrmecodia tuberosa* and *Hydnophytum montanum* are lined with mycelium. This is found only in tubers inhabited by ants; the free tips of the hyphæ are evidently bitten off by these insects and in some places the sods of mycelium are trimmed to an equal level. Mische believes that the fungus grows on the excrement of the ants, but he evidently discards the idea that the insects feed on it. If they cut the hyphæ down, it is merely, he thinks, because too thick a carpet would soon obstruct the galleries of the formicary. He thus regards the fungus as a mere intruder of no use to the ants. The presence of fungi inside myrmecodomatia seems to be very general, since Prof. Bailey found a more or less luxuriant growth inside the cavities of all the myrmecophytes of which he could obtain suitable material (See Part V). The mycelia are sporadically distributed in most cases, but their aerial portions show unmistakable evidences of having been cropped by the ants. In one of the species of *Plectronia* (*P. Laurentii*) and in the *Cuvieræ* there are dense mats of delicate, white hyphæ, which remind one forcibly of the "ambrosia" cultivated by certain wood-boring beetles and gall-midges, of which I shall have more to say below. In a recent paper, Bailey (1920) fully discusses the question whether the mycelia of the myrmecophytes are eaten by the ants and whether they are cultivated by them or are merely adventitious.

The pellets in the infrabuccal pockets of ants inhabiting myrmecophytes usually contain numerous spores and also fragments of hyphæ which appear to have been removed from the walls of the domatia. This might be considered as indicating that the ants feed to a greater or less

extent upon the fungi. But the evidence appears much less conclusive when viewed in the light of Bailey's discovery that the infrabuccal pellets of almost all ants tend to contain spores and fragments of hyphæ. This is as true of the entomophagous Ponerinæ and Pseudomyrmicæ as of the more or less omnivorous Myrmecinae, Dolichoderinæ, and Formicinae; of ants of temperate as of tropical regions; and of species which nest in the ground or in carton or silk domatia as of those which live in decaying plant tissue. On the other hand, such is not the case with the crops and stomachs of imaginal ants. If any of the ants actually feed upon fungi, they must triturate the spores and mycelia, or compress them, and drain off the liquid or semi-liquid contents. Under such circumstances, one would expect to find torn or ruptured spores and finely divided fragments of hyphæ in the infrabuccal cavity. This was not so, however, in any of the pellets analyzed by Bailey; the spores and fungus filaments were intact and still retained their protoplasmic contents. All the evidence at hand favors Janet's (1896, p. 15; 1899) contention that the function of the infrabuccal pocket is to serve as a receptacle for food-residues and detritus. Bailey therefore concludes that, though many ants are closely associated with fungi, there is no sufficient proof that any of the Formicidæ, other than the Attini, are fungivorous. The cropping of the hyphæ which cover the inner walls of myrmecophytes does not indicate necessarily that these fungi are eaten by ants.

In most myrmecodomatia the growth and sporadic distribution of the hyphæ suggest that the mycelia are purely adventitious. Only in the case of the localized luxuriant growths of "ambrosia" in *Cuviera* and *Plectronia Laurenti* are there indications that the ants may actually be fungus-farmers; the mycelia appear to be more or less pure cultures and are closely associated with the detritus of the ant colonies. Yet it is by no means certain that even these results are not obtained quite unintentionally on the part of the ants. The environmental conditions within the myrmecophytes undoubtedly facilitate the growth of fungi which must be kept within bounds by a constant cropping of the mycelia or they might interfere with the activities of the insects. Unless all fungi are equally resistant to continued cropping and react similarly in the peculiar conditions within the domatia, certain species will tend to become dominant. Should a particular form gain the upper hand and grow actively, it would probably be transferred to new nests by the queens, since the infrabuccal pockets of imagines almost invariably contain fragments of hyphæ or spores. Thus "pure cultures" of fungi may have been brought about through the activities of the ants, but

quite incidentally and without utilitarian purpose on the part of the insects. Such considerations are certainly of great interest in a discussion of the probable origin of the remarkable fungus-growing and fungus-feeding habits of the highly specialized Attini. If mats of hyphæ growing in particular luxuriance on the detritus (pellets, feces, etc.) of the colony were found by the ants to be edible, it would be a comparatively simple matter for these insects to increase the volume of their primitive fungus gardens by adding extraneous material, such as insect excrement or vegetable debris, to the original compost.

The systematic affinities of the fungi found flourishing on the inner walls of myrmecophytes have not been investigated. They probably represent imperfect forms of some of the higher Ascomycetes.

It is interesting to compare the fungus-growing behavior of the Formicidæ with like activities of other insects. Such are known at present to exist among the termites, or Isoptera, certain wood-boring beetles of the families Scolytidæ and Lyneuxyloniidæ, and a number of gall-making Cecidomyidæ.

That certain termites cultivate mushrooms in their nests was known long before similar observations were made with regard to ants, fungus gardens of the former having been accurately described in 1781 by Smeathman in his celebrated 'Account of the Termites.' Yet the true meaning of these gardens was not realized till after the fungicolous Formicidæ had been more fully investigated. Even at present, many aspects in the behavior of fungus-growing termites, such as the manner in which they feed on the mushroom and the origin of fungus gardens in their new nests, are still obscure. So much is certain — that their fungus-growing behavior differs from that of the Attini in several important particulars as summarized by Wheeler (1907, pp. 784-785).

In the first place the termites use their own excrement as a substratum, moulding it into the form of a sponge containing numerous habitable chambers and galleries. This substance is, of course, much harder and more compact than the comminuted leaves, etc., employed by the Attini. Second, the fungus grown on this substratum forms bromatia (the spherules or nodial heads) of a very different type from those found in the gardens of the Attini. And third, the termites that are in the habit of growing fungi are not exclusively mycetophagous like the Attini, but subsist also and probably very largely on dead wood, twigs and leaves.

According to Bugnion (1914a, p. 171), the larvæ and the royal pair alone are nursed with the bromatia of the fungus, while the adult workers and soldiers feed directly on vegetable fibres and cells. It may further be mentioned that the fungus-growing habit is by no means general in the

order Isoptera, but is restricted to certain paleotropical genera, such as *Microtermes* Wasmann and *Termes* Linnæus, which are regarded as the most specialized members of the group. As in the case of the fungus gardens of the Attini, the identity of the fungi grown by the termites is far from being known beyond question. The fungous sponges found in the termitaria are evidently imperfect forms of higher mushrooms, which have been ascribed to certain Basidiomycetes (Agaricaceæ) by Holtermann (1899), Doflein (1905*b*), and Petch (1906).

The so-called "ambrosia beetles" are all wood-boring Coleoptera whose larvæ do not feed directly on the fibres of the wood but on the bromatia of a fungus which the adults cultivate on the walls of their galleries. The best-known of these are certain Scolytidæ, which furthermore resemble ants and termites and differ from most other Coleoptera in that the adult beetles live in societies and care for and feed their larvæ. Perhaps the most interesting points in this case are that, so far as known, the food of each species of fungus-growing scolytid is limited to a certain kind of ambrosia and only the most closely related species have the same food fungus; also that the origin and further growth of the fungus is entirely under the control of the beetle. When the mother beetle leaves the old burrow to excavate new brood galleries, wherein to deposit her eggs, she transports with her the germs of the ambrosia fungus. Strohmeyer (1911) discovered lumps of mycelium adhering to the dense brushes of hair found on the head of the females of certain exotic Scolytidæ, these brushes being totally absent in the males; he believes that the fungus is transferred in this manner to the new burrows. In other ambrosia Scolytidæ, however, the females show none of these hair brushes, so that the fungus must be carried in some other way. According to Neger (1908*a-d*) the conidia of certain of these mushrooms form a mucilaginous mass which adheres readily to any part of an insect passing over it. In some cases part of the bromatia is preserved in the digestive tract of the adult beetle, and voided in the new burrow (Schneider-Orelli, 1913). The ethology of another wood-boring beetle, the European *Hylecatus dermestoides* (Linnæus), one of the Lymexyloide, has been studied by Neger (1908*a-d*, 1909*b*, and 1914) and more in detail by Germer (1912). These investigators have found that the larva, which burrows in dead tree stumps, never feeds on the wood itself. The walls of its galleries are overgrown with a mycelium producing globular bromatia and thick-walled spores, which are cropped off by the larva together with some of the hyphae. Since the female of *Hylecatus* lays her eggs on the bark of stumps and dies shortly after oviposition,

it is rather difficult to understand how the fungus in this case enters the larval burrows.

The ambrosia fungi of beetles are evidently very different from the mushrooms cultivated by ants and termites. According to Neger (1909b, 1914) and Beauverie (1910a-b), they belong to the Ascomycetes; the former has described the mushroom from the galleries of *Hylecatus* as *Endomyces hylecati* and it is possible that the ambrosia fungi of the Scolytidae are also related to the same genus.

The discovery that ambrosia fungi, similar to those cultivated by wood-boring beetles, grow inside the galls produced by certain gall-midges (Itonididae, formerly called Cecidomyiidae), was made by Beccharini (1893). He found that the galls formed by *Asphondylia spinosa* Rübssaamen on the flower buds of *Capparis spinosa* Linnæus always contain a mycelium. A few mycozooecidia—as Beccharini proposed calling them—have since been recorded in Europe, all being produced by species of the genus *Asphondylia*. Neger (1908a, 1909a, 1910b, and 1911a), who made extensive studies of these galls, found that the infections are by no means accidental, nor due to a parasitic or saprophytic fungus, and that the larvæ of the gall-midge feed on the mycelium. The spores are probably deposited on the plant by the female *Asphondylia*, together with the egg. Neger also recognized the great similarity between the fungi found in these galls and the "ambrosia" cultivated by certain Scolytidae. He therefore proposed the term "ambrosia-galls" for all cecidia normally containing hyphæ of mushrooms. In a number of cases artificial cultures could be obtained from these fungi, which, it was thus shown, belong to species of *Macrophoma* (Ascomycetes) not yet found outside the galls.

Many of the foregoing details have been taken from Wheeler's 'Fungus-growing Ants of North America' (1907), which gives a complete review of the fungus-growing behavior not only of ants but also of termites and ambrosia beetles. The reader is referred to this important paper for additional information on the subject.

Fungous Parasites of Ants

In the following account of the fungi which parasitize ants, I have left aside the endozoa Sporozoa and Schizomycetes, some of which are important agents of bacterial infections of caterpillars, bees, locusts, etc., but are not known or have not been studied among ants. Six families of true fungi, namely the Entomophthoraceæ, the Hypocreaceæ, the Laboulbeniaceæ, the Mucedinaceæ, the Stilbaceæ, and the Dematiaceæ,

contain forms which attack living insects. In some other groups, such as the Saprolegniaceæ and the Pythiaceæ, certain species are commonly met with on dead insects; these are, however, mere saprophytes and cannot be properly included among the entomogenous fungi.

From the data collected in this chapter, it is evident that ants are remarkably immune from the attacks of parasitic fungi; only a few species of such ant parasites are known and these are rarely encountered. This is the more surprising since ants exist everywhere in great abundance and have probably been collected and studied in larger numbers than any other group of insects.

At first sight ants would seem to be particularly favorable hosts for such parasites since these insects are in the habit of huddling together in masses in warm subterranean galleries, where the fungi might be supposed to develop luxuriantly and transmit their spores from ant to ant with great facility. Further consideration of the matter, however, leads to the conclusion that other habits of the ants must, in all probability, tend to suppress or render impossible the development of the fungi, except under unusual conditions. All ants devote a great deal of time and attention to cleaning their own integument and that of their nestmates. They are, indeed, forever combing and scraping the surfaces of their bodies with their tongues and strigils, so that fungi must find it difficult to gain a precarious foothold in their nests, to say nothing of an opportunity to proliferate. And even on the rare occasions, when this happens, important organs like the mandibles, antennæ, labium, maxillæ, palpi and eyes are kept scrupulously free from parasitic growth. (Wheeler, 1910a, p. 85.)

The ENTOMOPHTHORACEÆ constitute part of the very extensive class of alga-like fungi or Phycomycetes. By far the majority of the species of this family parasitize living arthropods, though a few genera grow on living or dead plants. "They are distinguished by the production of numerous hyphæ of large diameter and fatty contents, which, in the insect forms, ultimately emerge from the host in white masses of characteristic appearance and produce at their extremities large conidial spores which are violently discharged into the air and propagate the disease. The common house-fly fungus is perhaps the most familiar example of the kind, and no one can have failed to notice the affected flies in autumn or late summer adhering to looking-glasses or window-panes surrounded by a smoky halo of discharged conidia. In addition to these conidia the propagation of the fungus, after long periods of rest, may be provided for by the formation of thick-walled resting spores adapted to withstand successfully the most unfavorable conditions. These resting spores, which may be either sexual (zygospores), or asexual (azygospores), finally germinate and produce conidia that are discharged in the usual fashion and serve to infect fresh hosts." (Thaxter, 1888,

p. 136.) The parasitic forms in this family usually attack soft-bodied insects, such as flies, caterpillars, moths, butterflies, aphids, etc.; the infection results from contact with a conidial spore, which, adhering to the host, enters its body by means of a hypha of germination. These fungi have never been observed on ants, perhaps because they have not been properly looked for, though it is quite possible that the heavy, chitinous integument and the customary cleanliness of ants protects them against infection by such parasites.

The HYPOCREACEÆ belong to the class Ascomycetes, and among them several species of *Cordyceps* afford "by far the most conspicuous examples of entomogenous plants, many of which are of large size, or brightly colored" (Thaxter, 1888, p. 135). In this case, the polycellular mycelium pervades the tissues of the host, which is rapidly killed, and often produces asexual spores or conidia, borne on external hyphae variously agglutinated or united. In this imperfect, more common condition, they are often described under the generic designation of "*Isaria*" and are then placed, together with other similar imperfect fungi, in the family Stilbaceæ. The mycelium finally produces outside the body of the insect a boll-shaped or club-like organ or fructification, carried on a stalk sometimes several inches in length. The swollen portion of this external stroma bears numerous ascocarps or perithecia containing the spores, which are formed within elongate cells, the asci. As many as eleven species of *Cordyceps* have been described from ants, but some of these are very imperfectly known, especially with regard to the structure of the asci and spores, so that they are much in need of further study. Furthermore, all *Cordyceps* seem to be little or not particular in the choice of their host, the same species often growing indifferently on insects of several orders.

CORDYCEPS E. Fries

Cordyceps E. FRIES, 1818, 'Observ. Mycol. Flor. Succ.', p. 316.

Cordyceps australis (Spegazzini)

Cordyceps unilateralis subspecies *australis* SPEGAZZINI, 1881, An. Soc. Cientif. Argentina, XII, p. 80 (of separate).

Cordyceps australis SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.', II, p. 571. SPEGAZZINI, 1889, Bol. Ac. Nac. Ciencias Córdoba, XI, p. 536. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 31. MASSEE, 1895, Ann. of Botany, IX, p. 15; 1898, Revue Mycologique, XX, p. 86. A. MÖLLER, 1901 'Phycom. u. Ascom. Unters. aus Brasilien,' p. 218, Pl. vi. figs. 92 and 93.

Cordyceps australis P. HENNINGS, 1902, Hedwigia, XLI, p. 10.

This species seems to be rather common in southern Brazil, where it was originally discovered near Apiahy on *Pachycondyla striata* Smith by Puiggari, and later seen three times on the same species of ant at Blumenau by A. Moller. It has also been found in southern Brazil on various beetles.

***Cordyceps japonensis* Hara**

Cordyceps japonensis HARA, 1914, Botan. Magazine, Tokyo, XXVIII, pp. 348 and 351, fig. I.

Cordyceps species, HARA, 1913, Nawa's Insect World, Gifu, Japan, XVII, p. 472, figs. A-D.

Described from Japan: Province Mino, Kawauye-mura and Province Mino, Kakununo-ga-hara (K. Hara Coll.); growing on an unidentified ant, to judge from the description, a species of *Camponotus*.

***Cordyceps formicivora* (Schröeter)**

Torrubia formicivora SCHRÖETER, 1894, in Cohn, 'Kryptogamen-Flora von Schlesien,' III, 'Pilze,' 2, p. 276.

Cordyceps formicivora SACCARDO, 1895, 'Syll. Fungorum,' XI, p. 366.

Growing from the thorax of *Camponotus ligniperdus* (Latreille) on the Warthaberg, Frankenstein, Silesia (Schröeter Coll.).

***Cordyceps Lloydii* Fawcett**

Cordyceps Lloydii FAWCETT, 1886, Ann. Mag. Nat. Hist., (5) XVIII, p. 316, fig. SACCARDO, 1891, 'Syll. Fungorum,' IX, p. 1000. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 36, fig. 9. MASSEE, 1895, Ann. of Botany, IX, p. 20; 1898, Revue Mycologique, XX, p. 90. C. G. LLOYD, 1919 (June), Mycological Notes, No. 59, p. 856, fig. 1437.

This fungus was originally described from a specimen growing on *Camponotus abdominalis* (Fabricius), = *C. atriceps* (F. Smith), and found on the banks of the Puruni River, British Guiana (G. A. Lloyd Coll.). C. G. Lloyd has recently recorded it from Uganda, where it was obtained by W. Gowdey, growing on a dead worker of *Paltothyrcus tarsatus* (Fabricius) attached by means of its mandibles to the stalk of a plant: "The fungus is a very minute, white club with a small capitate head and seems to agree very well with the original figure." To judge from C. G. Lloyd's photographs, this parasite is very different from the *Cordyceps* commonly found in the Belgian Congo on the same ant, *Paltothyrcus*, and referred below to *C. myrmecophila* (Cesati).

Cordyceps myrmecophila (Cesati)

- Hypoecra (Cordyceps) myrmecophila* CESATI, 1846, in Klotzsch, 'Herb. Mycol., Centuria XI, cura L. Gravenhorst,' No. 1033 (exsiccata with description). D. v. SCHLECHTENDAL, 1846, Bot. Zeitung, IV p. 877. CESATI, 1855, *ibid.*, XIII, p. 75.
- Campylothecium myrmecophilum* CESATI, 1846, in Klotzsch, 'Herb. Mycol., Centuria XI,' No. 1033.
- Hypoecra myrmecophila* BERKELEY AND BROOME, 1851, Ann. Mag. Nat. Hist., (2) VII, p. 186.
- Cordyceps myrmecophila* CESATI, 1858, in Klotzsch, 'Herb. Mycol., Ed. Nov., Centuria VIII, cura L. Rabenhorst,' No. 719 (exsiccata with description). D. v. SCHLECHTENDAL, 1858, Bot. Zeitung, XVI, p. 302. M. J. BERKELEY, 1860, 'Outlines of British Fungology,' p. 382. W. NYLANDER, 1869, Notis. Sällsk. pro Fauna et Flora Fenn. Forhandl., X, p. 88, Pl. II, figs. 4a-d (separate in 1868). SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.,' II, p. 566. G. MASSEE, 1886, Grevillea, XV, No. 73, p. 2. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 31, fig. 6. MASSEE, 1895, Ann. of Botany, IX, p. 14; 1898, Revue Mycologique, XX, p. 85. RABENHORST, WINTER AND PAZSCHKE, 1890, 'Fungi Europaei,' No. 3649 (exsiccata). F. J. SEAVER, 1910, 'North American Flora,' III, pt. 1, p. 54. STITZ, 1911, Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08), III, p. 377, footnote. C. REA, 1914, Trans. Brit. Mycol. Soc., IV, pt. 2, (1913), pp. 199, 203, and 213.
- Cordyceps (Entomogena) myrmecophila* CESATI, 1861, Commentario della Soc. Crittogamol. Italiana, I, No. 2, p. 61, Pl. IV, figs. II, 1-4.
- Torrubia myrmecophila* M. C. COOKE, 1871, 'Handbook of British Fungi,' II, p. 771. PHILLIPS AND PLOWRIGHT, 1875, Grevillea, III, p. 126.
- Cordyceps myrmecophila* P. HENNINGS, 1904, Hedwigia, XLIII, 4, p. 248. STITZ, 1916, Ergebn. Zweit. Deutsch. Zentr. Afr. Exp. 1910-11. I, p. 371.

This is the most frequently observed fungous parasite of ants, being recorded from the tropical and temperate parts of both hemispheres and attacking many kinds of insects besides ants. It was discovered by Cesati in 1846, at Brescia, in Lombardy, Italy, some three hundred individuals of the same nest being infested by the fungus¹; the species of ant was not recorded at the time, but W. Nylander in 1869 identified Cesati's specimens—from Klotzsch's exsiccata—as *Formica fusca* Linnæus. W. Nylander mentions it also as occurring in Finland (Jalguba on Lake Onega; A. Kuhlhem Coll.), growing out of the anterior part of the pronotum of *Formica rufa* Linnæus. It was again noted by Hennings from Brazil (Rio Juruá, Juruá-Miry; E. Ule Coll.) on *Dinoponera grandis* (Guern).

In tropical Africa it seems to show a predilection for the common large ponerine ant, *Paltothyreus tarsatus* (Fabricius). Stitz (1911, p.

¹"Ce fut un cimetière de fourmis tout entier qui se parait de cette jolie Sphéridée." (Cesati, 1855, p. 75.)

377, footnote) mentioned the first African specimens growing on an ant of that species collected by Grauer in the forest near Kindu, Belgian Congo; and Schubotz also found it on the same ant in the Ubangi District. It is by no means rare, from my own experience and that of Messrs. Lang and Chapin, to find dead specimens of *Paltothyreus tarsatus* firmly attached with their closed mandibles to a leaf, a grass-stalk, or a stick, several inches or a few feet above the ground, while a long-stalked *Cordyceps* protrudes from the body. Though this position is often observed in ants that die from fungous diseases, it is nevertheless remarkable in this case since *Paltothyreus* is a predaceous, strictly terrestrial ant, not known to climb the vegetation normally. The stroma of the fungus grows out of the side of the thorax, as a rule between one of the coxal articulations. It is a slender stalk, 2 cm. or more long, and ends in a club-shaped fructification bearing the ascocarps. More rarely two such fructiferous stroma are borne by the same ant.

***Cordyceps proliferans* (P. Hennings)**

Cordyceps proliferans P. HENNINGS, 1904, *Hedwigia*, XLIII, 4, p. 248, Pl. iv, figs. 6 and 6a.

Cordyceps proliferans P. AND D. SACCARDO, 1905, 'Syll. Fungorum,' XVII, p. 825.

Described from Rio Jurua, Marmellos, Brazil, growing on *Dinoponera grandis* (Guerin) (E. Ule Coll.).

***Cordyceps Ridleyi* Massee**

Cordyceps Ridleyi MASSEE, 1899, *Bull. Misc. Inform. Bot. Gard. Kew*, Nos. 153-154, p. 173. SACCARDO AND SYDOW, 1902, 'Syll. Fungorum,' XVI, p. 613. CHIPP, 1921, *The Gardens' Bull., Straits Settlements*, II, p. 326.

Found in Selangor, Malay Federated States (Ridley Coll.), springing in considerable numbers from the head, thorax, abdomen, and legs of an unidentified ant; some imperfect stromata also on the antennæ. This is a small fungus, the stromata being 3 to 4 mm. high. According to Chipp (1921) the host is "*Formica gigas*."¹

***Cordyceps Sherringii* Massee**

Cordyceps Sherringii MASSEE, 1891, *Ann. of Botany*, V, p. 510, figs. 2-6 (on p. 509). M. C. COOKE, 1891, *Grevillea*, XX, No. 94, p. 39. MASSEE, 1892, *Bot. Centralbl.*, LI, p. 334; 1895, *Ann. of Botany*, IX, p. 27; 1899, *Revue Mycologique*, XXI, p. 1, Pl. CLXXXIII, figs. 5-9.

Cordyceps Sherringii M. C. COOKE, 1891, *Grevillea*, XX, p. 15.

Cordyceps Sherringii M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 35, fig. 8. SACCARDO, 1895, 'Syll. Fungorum,' XI, p. 366.

¹Probably *Camponotus (Dinomyrmex) gigas* (Latreille)

Grenada, West Indies (Sherring Coll.).

"Gregarious on an ant, springing from various parts of the body, most firmly attached to the frond of a fern by a dense mass of pale ochraceous mycelium."

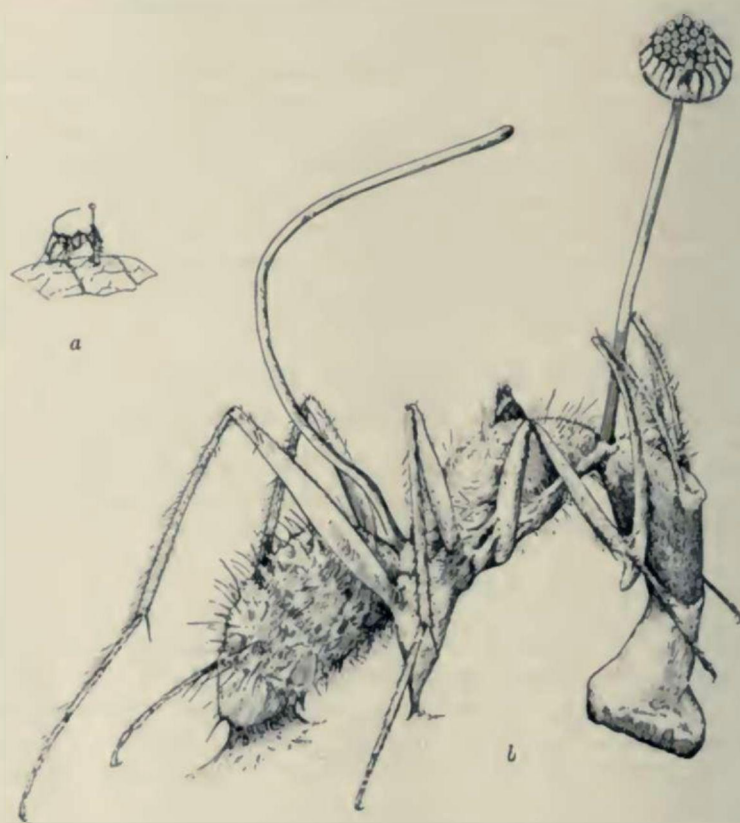


Fig. 77. *Cordyceps subdiscoidea* (P. Hennings) growing on *Camponotus (Myrmotherix) abdominalis* (Fabricius), at Kalacoon, Bartica District, British Guiana: a, natural size; b, $\times 10$.

***Cordyceps subdiscoidea* (P. Hennings)**

Cordyceps subdiscoidea P. HENNINGS, 1902, Hedwigia, XLI, p. 168.

Cordyceps subdiscoidea P. AND D. SACCARDO, 1905, 'Syll. Fungorum,' XVIII, p. 825.

This curious fungus was described from the confluence of the Para and Surinam Rivers, Dutch Guiana, on the thorax of an unidentified ant (J. Michaelis Coll.). Prof. Wm. M. Wheeler has recently found at Kalacoon, British Guiana, a beautiful specimen which I refer provi-

sionally to this species (Fig. 77), though it may be undescribed. It was growing on a dead worker of *Camponotus (Myrmotherix) abdominalis* (Fabricius), fixed on a leaf of a low bush in the forest near the Tropical Research Station of the New York Zoological Society.

***Cordyceps subunilateralis* (P. Hennings)**

Cordyceps subunilateralis P. HENNINGS, 1902, *Hedwigia*, XLI, p. 168; 1904, *Nerthus*, Pl. 1, fig. 9.

Cordyceps subunilateralis P. AND D. SACCARDO, 1905, 'Syll. Fungorum,' XVII, p. 826.

From the confluence of the Para and Surinam Rivers, Dutch Guiana, on the thorax of an unidentified ant (J. Michaelis Coll.).

***Cordyceps unilateralis* (L. and C. Tulasne)**

Torrubia unilateralis L. AND C. TULASNE, 1865, 'Selecta Fung. Carpologia,' III, p. 18, Pl. 1, figs. 3-4. BERKELEY AND COOKE, 1876, *Journ. Linn. Soc. London, Botany*, XV, p. 394.

Cordyceps unilateralis SACCARDO, 1883, 'Syll. Fungorum, Pyrenomyc.,' II, p. 570. FAWCETT, 1886, *Ann. Mag. Nat. Hist.*, (5) XVIII, p. 317. THAXTER, 1891, *Botan. Gazette*, XVI, p. 203. M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 33, fig. 7. MASSEE, 1895, *Ann. of Botany*, IX, p. 15; 1898, *Revue Mycologique*, XX, p. 86. SPEGAZZINI, 1912, *An. Mus. Nac. Hist. Nat. Buenos Aires*, XXIII, p. 76.

This is a rather generally distributed parasite of ants, and it attacks other insects too. Originally described from Brazil on *Atta cephalotes* (Linnaeus), it was again found there on the same ant by Traille.¹ Fawcett records it on *Camponotus abdominalis* (Fabricius), = *atriceps* (Smith), also from Brazil, and on *Echinopla melanarctos* Smith and *Polyrhachis merops* Smith, both collected by A. R. Wallace at Tondano, a village in the island of Celebes. Thaxter found it in North America on an ant which was not further specified at the time, but is, according to Prof. Wheeler's identification, *Camponotus herculeanus* (Linnaeus) subspecies *pennsylvanicus* (De Geer) from North Carolina.² Finally, Spegazzini mentions it from an unidentified ant found at Puerto León, Misiones, Argentina.

The external part of this *Cordyceps* consists of a black, very slender, thread-like stroma, 13 to 20 mm. long and $\frac{1}{4}$ to $\frac{1}{2}$ mm. thick at the base,

¹An unidentified *Cordyceps* is figured by J. R. Inda (1907, p. 4, fig. 2) on a leaf-cutting attine ant from Cuernavaca and Jolapa, Mexico.

²According to information kindly given by Prof. Wheeler, there are also in Prof. Thaxter's collection unidentified *Cordyceps* on *Camponotus herculeanus* subspecies *pennsylvanicus* variety *noroboracensis* (Fitch) from Maine, and on *C. abdominalis* (Fabricius) from Trinidad. An unidentified *Cordyceps* has also been mentioned on *Camponotus scryphallus* from Brazil by Fawcett (1886, p. 317).



Fig. 78. *Cordyceps unilateralis* variety *javanica* F. v. Hohnel, growing on *Camponotus* species, near Batavia, Java: a, ant with complete fungus, $\times 3.5$; b, capitulum of asei, $\times 7$; c, longitudinal section of capitulum showing perithecia, $\times 30$ (after v. Hohnel, 1909.)

feebly bent about or above the middle of its length, where it bears on one side the perithecia fused into a subglobose or hemispherical head, 1 to 2 mm. in diameter, with rosette-like protuberances.

***Cordyceps unilateralis* variety *javanica* F. v. Hohnel**

Cordyceps unilateralis variety *javanica* F. v. HOHNEL, 1909, Sitzb. Ak. Wiss. Wien, math. naturw. Kl., CXVIII, Abt. 1, p. 305, Pl., figs. a-h. SACCARDO AND TROTTER, 1913, 'Syll. Fungorum,' XXII, p. 512.

The stroma of this fungus (Fig. 78 a-c) was growing out between the head and thorax of an unidentified ant, probably, to judge from the drawing, a species of *Camponotus*, collected near Batavia, Java, by van Rozenburg.

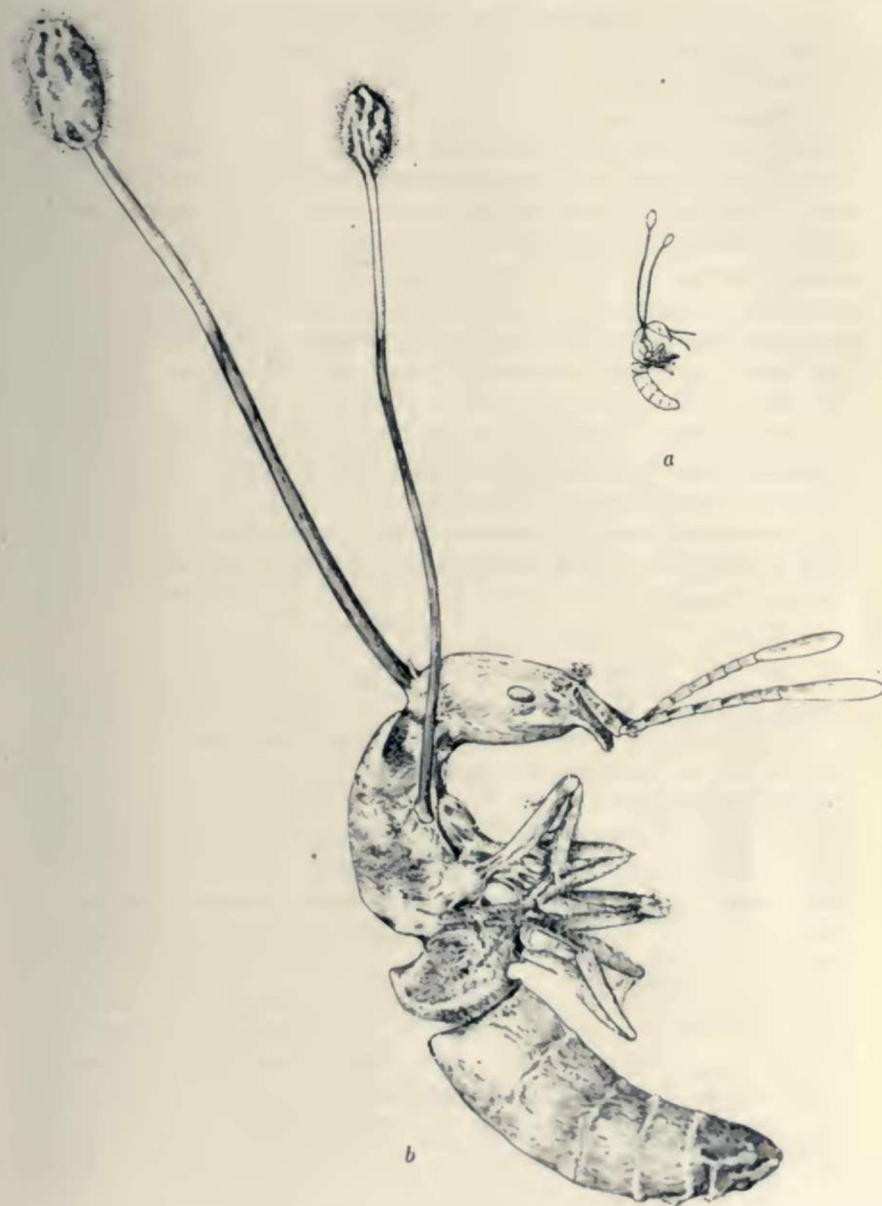


Fig. 70. *Isaria myrmecidarum* C. G. Lloyd, growing on *Pachycondyla striata* F. Smith, at Tijuca, in the vicinity of Rio de Janeiro, Brazil: a, natural size; b, $\times 25$.

Isaria myrmicidæ C. G. Lloyd

Isaria myrmicidæ C. G. LLOYD, 1920, Mycological Notes, No. 62, p. 915, Pl. CXLIII, figs. 1636 and 1637.

The above name is given by C. G. Lloyd to a parasite found in Brazil by J. Rick on an unidentified ant; his figure evidently represents the petiole and gaster of a ponerine, perhaps of the same species of *Pachycondyla* mentioned below as host of this fungus. The brief description reads as follows: "This is not a *Cordyceps* as would appear from the photograph but an *Isaria* which is only named for convenience in the museum. Our figure (Fig. 1636) enlarged six-fold tells all to be told about it. Fig. 1637 is natural size. The stem is about a centimeter long, slender and black. The head is cylindrical and white. Spores are 'pip-shape,' 2×8 ."

Fig. 79 shows a parasite of *Pachycondyla striata* F. Smith,¹ which is evidently Lloyd's "*Isaria myrmicidæ*." The drawing was made from a specimen in the Herbarium of the New York Botanical Garden kindly loaned to me by Dr. N. L. Britton and Dr. F. J. Seaver. It was obtained by J. N. Rose and P. G. Russell in 1915 at Tijuca, in the vicinity of Rio de Janeiro, Brazil.

Stilbum formicarum Cooke and Massee

Stilbum formicarum COOKE AND MASSEE, 1889, Grevillea, XVIII, No. 89, p. 8.
M. C. COOKE, 1892, 'Vegetable Wasps and Plant Worms,' p. 38, Pl. I, fig. 12.

An undetermined species of ant, sent from Cheltenham, Victoria, Australia, was bearing upon its body a little *Stilbum*, with elongated slender stems, from five to eight millimeters in length, black, and flexuous, slightly thickened towards the base, and bearing at the apex an obovate, pink-colored capitulum or head, with elliptical conidia (10μ long and 3μ broad). Several of these fungi occurred on the body of each dead insect.

The genus *Stilbum* comprises imperfect fungi, usually placed in a family STILBACEÆ. Most of the species are saprophytic and only a few have been found on insects. It is quite possible that the Australian form mentioned here represents the conidial form of some ant-attacking *Cordyceps*, and I have, therefore, thought it convenient to mention it in connection with the Hypocreaceæ.

¹The ant was identified by Prof. Wheeler.

The LABOULBENIACEÆ or Laboulbeniales constitute by far the most highly specialized and most interesting of fungoid parasites of insects. All are found growing on living arthropods exclusively. The family is usually included among the Ascomycetes and, even in his most recent papers, Thaxter sees no sufficient reason why it should not be placed in the Pyrenomycetes. Because of their combining in some respect peculiarities of the true Ascomycetes with others shown by certain Algæ of the class Floridææ, certain mycologists suggest that these fungi be considered as a class of themselves, for which the names Phycascomycetes or Laboulbeniomycetes have been used.

The following brief account of the Laboulbeniaceæ is adapted from R. Thaxter's admirable monographic studies of these plants and will, it is hoped, enable entomologists to recognize them without difficulty. Unlike the *Cordyceps* described above, they are inconspicuous and, when examined *in situ* on the host insect, appear in general like minute, usually dark-colored or yellowish bristles or bushy hairs, projecting from its chitinous integument either singly or in pairs, more commonly scattered, but often densely crowded over certain areas on which they form a furry coating. When studied with a proper magnification, the structure of a fully developed parasite corresponds to the following general scheme.

A (polycellular) main body, or *receptacle*, is fixed by means of a blackened base, or *foot*, to the integument of the host, and consists in most cases of a very small number of cells differently arranged in different genera. This receptacle gives rise above to certain peculiar appendages of very variable form, commonly connected with the production of the male sexual organs; while from the same individual, with few exceptions in which the plants are dioecious, female organs are also variously produced from which *perithecia* are eventually developed. In the perithecia, which may arise singly or in considerable numbers from a given individual, and which are quite remarkable in structure, are produced the reproductive bodies or *ascospores* that are formed in *asci* identical in all respects with the organs thus named in other members of the great group of ascomycetous fungi. The ascospores thus formed germinate on the surface of the host to which they become attached by a blackened modification of their basal extremity, and, without the formation of any hyphæ, grow directly to new individuals by means of successive cell divisions. (Thaxter, 1896, p. 198.)

Perhaps the most remarkable peculiarity of the Laboulbeniaceæ is their ability to thrive freely on their host without interfering much with its activity, inflicting little if any appreciable injury. The parasitism is external and, except in rare instances in which the foot sends into the body a rhizoid-like haustorium, the parasite derives its nourishment through a at most slight perforation of the host's integument. Indeed, so feeble are the ill-effects of their parasitism that the idea has at one

time been advanced these fungi be mere saprophytes, not feeding on their host but absorbing from the surrounding humid air such elements as are needed for their development (Cavara, 1899). Riek (1903), commenting upon the abundance of *Rickia Wasmannii* in some ant colonies, goes even a step further. "The animals," he writes, "apparently suffer but little or almost not from the fungus; one finds decidedly populous colonies which are much attacked. Possibly the animals may even derive some benefit from the fungus. It is not much out of the question to think of a kind of symbiosis, though I cannot for the present give any further indication concerning this point. Perhaps the fungus could be of advantage to the ants in providing them with sugar."

There is, however, not the slightest proof for Riek's surmise that the fungus is of any real use to its host, while there is plenty of evidence that the Laboulbeniaceæ are true parasites. "The rigid limitation of species of Laboulbeniales to single genera or even species, of insects, which holds in general throughout the group, could hardly, it would seem, be explained on the basis of pure saprophytism; and although, as previously stated, the growth of these plants is not associated with any appreciable injury to the host, it is nevertheless a true parasitism of a typically obligate type." (Thaxter, 1908, p. 223.) Moreover, the exact manner in which the fungus derives its food from its host is still not quite clear. The occurrence of a number of rhizoidal forms seems to render it certain that all Laboulbeniaceæ feed on the juices of the insect; in the ant parasites, as in a majority of cases, these nutritive elements are absorbed, without penetration, through the sucker-like foot (Thaxter, 1908, p. 248). According to Ceppe (1914, p. 396), the fungus takes from the superficial layers of chitin certain carbohydrates which are localized there (glucose and glycogene).

The greater number of Laboulbeniaceæ attack beetles, especially of the family Carabidæ; they are much rarer on other insects and only the three following species have hitherto been recorded from ants. They are among the smallest members of the family, not exceeding one-tenth of a millimeter in total length in the North American *Laboulbenia formicarum*; the two other forms being slightly larger.

Rickia Wasmannii Cavara

Rickia Wasmannii CAVARA, 1899, *Malpighia*, XIII, p. 182, Pl. vi. RIEK, 1903, *Österreich. Bot. Zeitschr.*, LIII, p. 163, fig. THAXTER, 1902, *Proc. American Ac. Arts Sc. Boston*, XXXVIII, p. 39; 1908, *Mem. American Ac. Arts Sci. Boston*, XIII, pt. 6, p. 248, Pl. xxxiv, figs. 1-13. CEPPE AND PICARD, 1909, *Bull. Scientif. France et Belgique*, XLII, p. 252. PICARD, 1913, *Bull. Soc.*

Mycolog. France, XXIX, p. 511. SPEGAZZINI, 1914, Redia, X, (1915), p. 29, Pl. 1, fig. 2. REHM, 1903, Ascomyceten, No. 1451 (exsiccata).

This is apparently the only fungous ant parasite commonly found in Europe. Originally described from Linz on the Rhine, Germany, where Wasmann found it on *Myrmica lævinodis* Nylander, it was observed by Rick on the same ant at several other localities in Luxemburg (Belle Vue), Germany (Berncastel on the Moselle), and Austria (Feldkirch and Garina in the Vorarlberg). Spegazzini mentions it from Italy on *Myrmica scabrinodis* Nylander

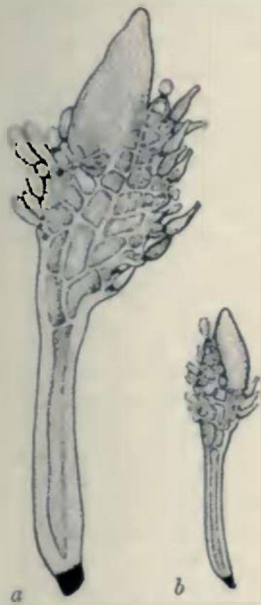


Fig. 80. *Rickia Wasmanni* Cava. a parasitic fungus of *Myrmica lævinodis* Nylander in Europe. Mature individual: a, $\times 600$; b, $\times 200$ (after Thaxter, 1908).

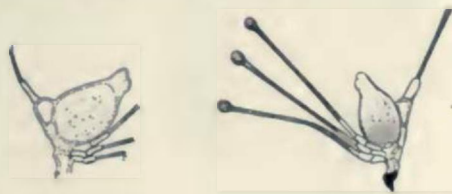


Fig. 81. *Rickia formicicola* Spegazzini, a parasitic fungus of *Prenolepis silvestrii* Emery in Argentina. Two mature individuals, $\times 300$ (after Spegazzini, 1917).

Rickia formicicola Spegazzini

Rickia formicicola, 1917, SPEGAZZINI, An. Mus. Nac. Hist. Nat. Buenos Aires, XXIX, p. 665, fig. num. 195.

This species (Fig. 81) was found in the island of Santiago, La Plata, Argentina, growing on *Prenolepis silvestrii* Emery.

Laboulbenia formicarum Thaxter

Laboulbenia formicarum, 1902, THAXTER, Proc. American Ac. Arts Sci. Boston, XXXVIII, p. 39; 1908, Mem. American Ac. Arts Sci. Boston, XIII, No. 6, p. 359, Pl. LVIII, figs. 14 and 15. WHEELER, 1910, Psyche, XVII, pp. 83-86. J. BEQUAERT, 1920, Bull. Brooklyn Ent. Soc., XV, p. 71.

This parasite (Fig. 82a-b) attacks various species of North American ants; strange to say, it has only been recorded thus far from the vicinity of Boston, where it appears to be rather common. Thaxter discovered it at Cambridge, Massachusetts, on *Lasius niger* variety *americanus* Emery and *Formica subpolita* variety *neogagates* Emery. Wheeler found the same fungus infesting nearly all the nests of *Lasius niger* variety *neoniger* Emery, on the seashore at Ellisville, Massachusetts, and gives some interesting details with regard to the ecology of the infested colonies.



Fig. 82. *Laboulbenia formicarum* Thaxter, a fungous parasite of various North American ants. Mature individuals: a, $\times 625$; b, $\times 260$ (after Thaxter, 1908).

On the beach itself, which consists of a deep layer of pure sand, there are colonies of *Formica fusca* variety *argentata* Wheeler, *Myrmica scabrinodis* Nylander variety *sabuleti* Meinert, *Tapinoma sessile* Say and *Lasius neoniger*. The last is far and away the most abundant and its workers are of large size. None of the ants in this locality, including the *neoniger*, was found to be infested with Laboulbeniaceæ. On the border of the salt meadow, however, immediately adjoining the beach, where the soil is moist, consisting of a mixture of rather sour, decomposing humus mixed with sand, and probably not infrequently wetted by the spray and occasionally even submerged at very high water, the only ant is *L. neoniger*, but its colonies are less populous than those on the beach, the workers are distinctly smaller and are practically all infested with the *Laboulbenia*. Passing over from this zone of infestation to the pasture land adjoining the salt meadow, the variety *neoniger* is replaced by *L. niger* L. variety *americanus* Emery which is the form of the species commonly occurring in higher and dryer pastures and fields. None of the workers of this form, which lacks on the scapes and legs the erect hairs so conspicuous in the variety *neoniger*, was found to be infested with the fungus. It would seem, therefore, that while *neoniger*, unlike any of the other ants, is able to exist in a depauperate condition in the damp, sour soil at the edges of salt meadows, it does so only at the risk of becoming infested with *Laboulbenia formicarum*. Indeed, the infestation of the ants in this strip of littoral at Ellisville is often so excessive that they resemble hedgehogs, fairly bristling with tufts of the fungus. (Wheeler, 1910a, p. 84.)

Though *Laboulbenia formicarum* may occur on all parts of its host, it appears from Wheeler's observations that it grows most abundantly on the abdomen, middle and hind femora and tibia, and posterior portions of the head. The thorax and coxæ, as a rule, are entirely free from the fungus; the clypeus and gula are generally free, and this seems to be invariably the case with the mandibles, antennal funiculi, palpi, labium,

maxillæ, and eyes. In a very few specimens, one or two of the little plants were seen on the antennal scapes, but, as a rule, these organs are perfectly clean.

In August 1919, I took a worker of *Formica pallide-fusca* subspecies *schaufassii* Mayr infested with *Laboulbema formicarum* at Forest Hills near Boston. I was, however, unable to locate the nest to which this individual belonged, but this observation shows once more that this fungus, though restricted to ants, attacks indifferently many species (Bequaert, 1920). Prof. Thaxter has also informed Prof. Wheeler that he has taken this *Laboulbenia* on various species of *Formica*, at Cambridge, Massachusetts.

Several so-called "imperfect fungi"—incompletely developed, conidia-bearing or sterile stages of various Ascomycetes—are known to attack insects, and some of these have been seen on ants. I have mentioned above *Stilbum formicarum* Cooke and Masee and have also alluded to the *Isaria* stage of *Cordyceps*, which may be expected on ants, since so many species of the latter genus have been found in the ascibearing stage on these insects. H. Bischoff (1912) has mentioned the finding by Quiel, at Potsdam, Germany, of two nests of *Formica rufa* heavily infested with fungous growths, about the size of a pin-head and attached mainly to the thorax, more rarely to other parts of the body. The ants were apparently but little hampered by their parasites. From cultures obtained with these fungi, Bischoff concludes that they belonged to several species, among them a *Mucor* (of the *spinulosus* group), a *Penicillium*, and a yeast with sexual reproduction; characteristic brown hyphæ present in the tufts on the ants, were not obtained in the cultures. More recently, Thaxter (1914, p. 239) found in the vicinity of Cambridge, Massachusetts, a fungus forming blackish incrustations on various parts of ants, and giving rise to a few short, colorless, erect branches; the exact nature of this plant has not been determined, nor is the name of its host mentioned.¹

Thaxter (1891, p. 203, Pl. xx, figs. 1-9) has described, under the name *Desmidiospora myrmecophila*, a new genus and species of fungus which was growing luxuriantly on a large black ant fastened to the under side of a rotting log in Connecticut.² The hyphæ, much branched and septate, covered the host in a white flocculent mass; they emerged

¹J. Leidy (1884) has recorded finding in Pennsylvania a *Camponotus pennsylvanicus* under the bark of a decaying tree; it was infested with a fungus which spread through every part of the body. This may have been a saprophytic fungus which had invaded the ant after death.

²This ant has recently been identified by Prof. Wheeler in Prof. Thaxter's collection as *Camponotus herculeanus* subspecies *pennsylvanicus* (DeGeer). Prof. Thaxter also possesses the same fungus from New Hampshire, growing on the subspecies *pennsylvanicus* and its variety *noveboracensis* (Fitch).

especially from between the abdominal segments, enveloping the insect more or less completely and extending a short distance over the substratum. The spores are of two kinds, the microconidia being minute ($12 \times 2 \mu$), hyaline, subfusiform, and produced at the apex of subulate lateral basidia; while the macroconidia are much larger, terminal, brown, flat, multilocular, irregularly lobed, up to $\frac{1}{10}$ mm. broad ($80-100 \times 68-90 \mu$ and $12-14 \mu$ thick). Thaxter remarks that it is not impossible that this fungus is an imperfect form of some *Cordyceps* or possibly parasitic on an immature *Isaria* or *Cordyceps* previously developed within the insect. As it is, Thaxter places *Desmidiospora* among the Hyphomycetes and Lindau¹ regards it as genus of the Mucedinaceæ. Some years ago Patouillard (1892) described, under the name *Hirsutella entomophila*, a curious fungus found growing on a beetle in Ecuador. At first sight it resembled an *Isaria*, but Patouillard thought he had observed that the spores were borne on basidia; he, therefore, included this parasite among the Basidiomycetes, placing it in the Clavariæ. Recently, however, Speare (1920) has shown that this, as well as similar fungi, do not produce true basidia and must be removed from the Basidiomycetes. It is rather a definite form of imperfect fungi, probably a stage of one or more species of *Cordyceps* or related genera. In the same paper, Speare remarks apropos of *Desmidiospora myrmecophila* Thaxter (p. 65): "While its resting spores are anomalous in character, and although no structures analogous to the synnemata of *Hirsutella* were described, its subulate sporophores and fusoid spores are of the same type as the corresponding organs of the form under consideration."

A snowy white mould, *Sporotrichum minimum* Spegazzini (1881, pt. 4, p. 123 of reprint; Saccardo, 1886, p. 101; M. C. Cooke, 1892, p. 37), also one of the Mucedinaceæ, was found in Argentina upon the putrescent body of *Acromyrmex lundii* (Guerin), in a rotten trunk. It was diffused over the insect, at first in a powdery and then a cottony white stratum, forming minute tufts. The threads were creeping and densely interwoven, branched, very slender (scarcely 2μ in diameter), sparingly septate, hyaline, with conidia scattered here and there.

It is possible that both this *Sporotrichum* and Thaxter's *Desmidiospora myrmecophila* are mere saprophytes, which have grown over the ant after the death of the insect.

Hormiscium myrmecophilum Thaxter, another imperfect fungus found on ants, is described by Thaxter (1914, p. 238, Pl. XIX, figs. 22-25) as follows: "Filaments nearly hyaline, becoming brownish, darker near

¹In Engler and Prantl, 1900, Die Natürl. Pflanzenfam., I, Abt. 1**, p. 454.

the base, closely septate, the cells often as broad as, or broader than long, undifferentiated, distally bluntly rounded, erect or curved upward, rigid, simple, less frequently sparingly branched, tapering but slightly if at all, one to several arising from a deeply blackened foot of variable size and shape. Maximum length about 280μ by $7-8\mu$ in width."¹ It was found on various parts of a species of *Pseudomyrma* collected by W. M. Mann along the Amazon River, Brazil; the majority of the individuals taken from a nest were infected by the fungus, which is sufficiently large to be readily visible as it projects from the surface of the host. It produces no differentiated cell-groups or definite spores, as far as has been observed, and appears to propagate itself by fragmentation only, the filaments proliferating after a terminal portion has been broken off. The opaque and somewhat variable foot, by which the individuals are attached to the surface of the host, appears to correspond to such a small fragment broken from a hypha, which, adhering laterally, becomes blackened and indurated, and gives rise to new filaments, while at the same time it serves the office of attachment as well as of food absorption. The other members of the genus *Hormiscium* are saprophytic, being mostly found on decaying vegetable matter; it is placed in the family Dematiaceae among the Hyphomycetes.

Finally, I must mention that Donisthorpe, in his treatise of British ants (1915, p. 235, fig. 86; see also Donisthorpe, 1913, pp. 96-97), figures a worker of *Lasius umbratus* variety *mirto-umbratus* Forel with patches of algæ on body and legs. Concerning this parasite, he expresses himself as follows:

On August 11th, 1912, when at Weybridge in company with Professor Wheeler, we found two colonies of this variety, very many of the ants of both being infested with a curious dark brown warty growth in patches on parts of the body and legs—this Wheeler thought might be a fungus which was unknown to him. I kept a number of these ants in captivity, and added uninfected workers of *umbrata* from other localities; the growth however did not increase nor spread to the new ants, but rather seemed to decrease. I sent some of the infested ants alive and others in spirit, to Dr. Baylis Elliott, and she considered the patches were colonies of unicellular organisms growing on the outside of the ants; eventually she came to the conclusion that they were not fungoid growths, but probably colonies of an alga.

Intracellular Bacteria of Ants

In various groups of insects unicellular organisms of a fungous or bacterial nature have been discovered inside certain cells of the body. They are apparently not parasites, but must rather be considered as

¹*Hormiscium pituophilum* variety *murmecophilum* J. B. Elliott (1915, pp. 130-142) is an entirely different fungus, which was found growing on the carton walls of certain nests of *Lasius umbratus* in England (p. 379).

living in symbiosis with their host. Special devices, often of a complicated nature, assure their transmission within the insect egg from one generation to another, so that they have become normal constituents of all the members of certain species, genera, families, or even higher groups of insects. Some of these micro-organisms float freely in the lymph, and in many cases great numbers of them also fill the plasma of certain fat-cells, thus forming so-called "mycetocytes." The mycetocytes may occur isolated in various parts of the body, or they may be grouped together and even more or less fused into special fungous organs, the "mycetoms." Sometimes micro-organisms of two or even three different kinds live within separate cells of the same host, either quite apart from one another or in compound mycetoms. Typical illustrations of intracellular mycoses are presented by certain hemipterous insects. In particular, all the Homoptera possess such intracellular, hereditary symbionts; their mycetoms are often enclosed within a pigmented epithelium and connected with special branches of the tracheal system of the insect (P. Buchner, 1913).

Intracellular symbionts also occur in certain ants, and it is probable that their presence in these insects is more frequent than is known at present. They were first seen by Blochmann (1884, 1888) in *Camponotus herculeanus* subspecies *ligniperdus*, densely filling cells which this investigator regarded as belonging to the epithelium of the intestine. According to Buchner's recent researches (1919) the intracellular organisms of that ant are really contained in special mycetocytes placed in a continuous layer beneath and between the true epithelial cells of the mid-gut. They are present in all individuals in the form of tiny, thread-like bodies, 10 or 12 μ long, generally regarded as bacteria. At the beginning of the sexual maturity of the insect, some of the symbionts leave their mycetocytes, in the worker as well as in the queen. They invade the egg-follicles from all sides and penetrate the egg, the entire plasma of which at first becomes densely filled with bundles of bacteria placed parallel to one another; but, as the egg grows, these organisms are pushed to its posterior pole. Blochmann found similar, but smaller (4 to 5 μ), organisms in *Formica fusca*, where they occupy two groups of cells in the adipose tissue. According to Buchner (1918, p. 77, footnote), intracellular bacteria live in many species of *Camponotus*, such as *C. senex* (F. Smith), *C. maculatus* subspecies *congolensis* Emery, *C. maculatus* subspecies *brutus* (Forel), *C. maculatus* subspecies *atramentarius* Forel, *C. rectangularis* subspecies *rubroniger* Forel, and perhaps in all the members of that genus. But they are absent in many other ants, as, for instance, in *Myrmecina latreillei* Curtis.

2. A REVIEW OF AFRICAN MYRMECOPHYTES

For all practical purposes, ant-plants or myrmecophytes may be briefly defined as plants which during life are continuously inhabited by certain species of ants. This definition, however, calls for certain explanatory remarks which will be found in the introduction to the general review of recorded ant-plants (p. 494). What is known of the ecology of African myrmecophytes has been brought together in the present chapter, in addition to my own field observations. For the convenience of the entomologist, I have compiled from the taxonomic literature the technical descriptions of these plants. To most students they will, I fear, not be much more helpful than they were to me; but descriptive botany seems able to offer nothing better. In themselves, they afford sufficient apology for the fact that in so many cases a correct identification of the plant in question can not be made.¹ It is to be hoped that the absence of a specific name will not render the observations recorded entirely valueless, since more often than not future field workers will be able to recognize the plants by some of the peculiarities shown in the drawings or mentioned in the text.

Being more familiar with the African flora, I may be permitted to call attention to a few general features of myrmecophytism as suggested by a consideration of African ant-plants. Certain of these remarks may also apply to myrmecophytes of other regions, while some perhaps could not be generalized without modification.

(a) Though over 30,000 species of flowering plants have been described thus far from the Ethiopian Region, only 42 of them can be regarded as more or less well-defined or probable myrmecophytes. In not more than 20 of these cases have the relations to ants been established from actual observation; for the remaining 22 species myrmecophily is merely surmised from analogy with what is known of their near relatives.² In other tropical parts of the world, the number of plants with special accommodations for sheltering ants is somewhat higher (about 116 species in the Neotropical and 109 species in the Indomalayan, Papuan, and Australian Regions), but it must be remembered that their floras are much richer than that of the Ethiopian Region, so that their proportion of myrmecophytes is but little if any higher. The compara-

¹In the case of plants collected by me, numbers are given referring to my herbarium specimens which are now in the hands of Prof. E. De Wildeman, Director of the Brussels Botanical Garden. Some of these specimens have been identified by that authority and their study will undoubtedly be completed in the near future.

²Sixteen myrmecophytes are at present known from the Belgian Congo. According to the latest data available, 6372 species of Spermatophyta, belonging to 1261 genera, had been described from that region at the end of 1918 (Gossens, V. 1919. 'Aperçu de nos connaissances actuelles sur la flore du Congo belge.' Bull. Agric. du Congo Belge, X, pp. 154-161).

tively small number of myrmecophytes is rather surprising considering the abundance and variety of tropical plant life and the many opportunities which ants must have had to become acquainted with it.

(b) The African myrmecophytes belong to a few taxonomic types, represented by 7 families and 12 genera, as follows:

Leguminosæ	<i>Schotia</i> , with 1 species.
Euphorbiacæ	<i>Macaranga</i> , with 2 species.
Sterculiacæ	<i>Cola</i> , with 3 species.
	<i>Scaphopetalum</i> , with 2 species.
Flacourtiacæ	<i>Barteria</i> , with 5 species.
Apocynacæ	<i>Epitaberna</i> , with 1 species.
Verbenacæ	<i>Vitex</i> , with 2 species.
Rubiaceæ	<i>Uncaria</i> , with 1 species.
	<i>Sarcocephalus</i> , with 1 species.
	<i>Randia</i> , with 3 species.
	<i>Plectronia</i> , with 6 species.
	<i>Cuviera</i> , with 15 species.

Schotia, *Cola*, *Scaphopetalum*, *Barteria*, *Epitaberna*, and *Cuviera* are precinctive Ethiopian genera, while the others are either also represented in the Oriental and Indomalayan Regions (*Macaranga*, *Sarcocephalus*, *Plectronia*) or tropicopolitan (*Vitex*, *Uncaria*, *Randia*). The family Rubiacæ leads the list with the largest number of myrmecophilous species (26, belonging to 5 genera), which is true also in other tropical regions. For *Barteria*, *Epitaberna*, and *Cuviera*, myrmecophytism is to all appearances one of the generic peculiarities, probably being present in all the members.

It is a curious fact that in the Ethiopian Region and elsewhere some of the largest families of the vegetable kingdom, in which differentiation into species has been most active, show very few (Leguminosæ, Orchidacæ) or no cases of myrmecophily. As illustrations of the latter may be mentioned the Gramineæ, Cyperacæ, Liliacæ, Labiatæ, and Compositæ.

(c) True myrmecophytes are restricted to the sections of the earth situated between the tropics, a fact easily accounted for by the uniform temperature which prevails there and permits ants to establish their perennial abodes within the rather thin walls of plant tissues. I already have shown (p. 371) that the so-called ant acacias of the dry East African plains and *Clerodendron formicarum* of the savannah country are by no means myrmecophytes. When these cases are eliminated, all African ant-plants known at present occur only in the permanently moist and ever-green Rain Forest of the western and equatorial parts of the continent. All the Oriental and Indomalayan and the vast majority of the Neotropical myrmecophytes grow similarly in the moist tropical forest areas.

The one notable exception is presented by the true ant acacias of Central and South America (p. 510), which do not grow in the forests, but only in the open country or savannahs and along road-sides, and in some cases even prefer semiarid regions.

(d) The African myrmecophytes are all perennials and of a woody texture, either bushes, low trees, or woody creepers. This also holds true for the ant-plants of southern Asia, Malasia, and tropical America, though the types there are somewhat more varied, including, for instance, typical epiphytes. It is essential to the prosperity of the ant colonies that their permanency be assured for many years, a condition which, of course, could not be provided by annual or biennial plants. In addition, the woody texture of the walls adds considerably to the solidity of the domatia and to the protection of the formicaries. In a number of cases (*Cola*, *Scaphopetalum*), but not all, the leaves and stems of plants inhabited by ants are abundantly covered with long, stiff hairs.

(e) The structures offered as myrmecodomatia by the ant-plants show but little diversity, are usually of a very simple type, and affect few organs of the plant. There is nothing here comparable with the intricacy and endless variety of adaptations presented by entomophilous flowers to pollinating insects. The following types of myrmecodomatia have been recognized in Africa.

1.—The stipules persist for some time and are much swollen, their recurved margins enclosing a pouch-like cavity: *Macaranga saccifera*. A more primitive condition of stipular myrmecodomatia is illustrated by the *Uragoga* described on p. 453.

2.—The leaves produce pouches at the base of the blade: species of *Cola* and *Scaphopetalum*.

Swollen stipules and leaf pouches may be regarded as myrmecodomatia of a very primitive type. They are not much sought by the ants, probably because they do not offer enough solidity and permanency as shelters for formicaries. In the few cases in which I observed ants using the swollen stipules of *Macaranga saccifera* and the foliar pouches of *Cola Laurentii* and *Scaphopetalum Thonneri*, the colonies were very small and the ants timid.

3.—The stems of the plant are externally normal, but hollowed out practically their entire length: *Vitex Staudtii* and *Barteria Deweveri*.

4.—The stems present fistulose swellings either in the middle of the internode, (*Randia Lujæ* and *R. myrmecophyla*), in, above, or below the nodes (*Uncaria*, *Sarcocephalus*, *Plectronia*, and *Cuviera*), or at the base of certain branches (*Barteria fistulosa*).

In other tropical regions there are a number of additional types not yet recognized in Africa, such as stipular thorns (*Acacia*), swollen petioles (*Tachigalia*, *Nepenthes bicalcarata*), pitcher-shaped leaves (*Dischidia*), inflated leaf-sheaths (*Korthalsia*), hollowed pseudobulbs (*Schomburgkia*), and fistulose rhizomes (*Polypodium sinuosum*, *Lecanopteris carnosa*, *Myrmecodia*, etc.)

In the case of stipular or leaf pouches, the slit which leads into the cavity is a natural result of the production of the pouch. In all other African myrmecophytes, there is no preformed entrance to the domatia and the apertures are gnawed by the ants.

(f) A very small number of African ants have become adapted to nesting in the domatia of ant-plants. A distinction should be drawn here between OBLIGATORY plant ants, that live exclusively in myrmecophytes, and species which are only occasionally or accidentally associated with these plants and may therefore be designated as FACULTATIVE (Wheeler, 1913, p. 115). Most of the African plant ants fall in the second group; they belong to such genera as *Crematogaster*, *Tetraoponera*, *Monomorium*, *Leptothorax*, *Tetramorium*, *Cataulacus*, *Technomyrmex*, and *Prenolepis*, which are abundant in the forest, usually leading an arboreal or semi-arboreal life; many of the species make no distinction between cavities of dead or living plants wherein to shelter their formicaries. *Viticicola tessmanni* and the two species of *Pachysima* (*P. æthiops* and *P. latifrons*) are the only African obligatory plant ants. They have never been found away from their hosts, *Vitex Staudtii* in the case of *Viticicola* and various species of *Barteria* and *Epitaberna myrmecia* in the case of the *Pachysimæ*. It is possible that certain African species of *Engramma* and *Plagiolipsis*, which have been collected only in plant domatia, are also of the obligatory type, but their case calls for further investigation.

There are a number of doubtful cases of myrmecophily among African plants and also others that are based on erroneous or incomplete observations. Some of these have been dealt with in the present paper under their respective families or genera, but a few others must be briefly mentioned here for the sake of completeness.

Stereospermum dentatum Richard (Bignoniaceæ), of Abyssinia and Kordofan. According to Penzig (1894) the pith in the upper part of a flowering branch is excavated for a space of one or two internodes and the cavity is inhabited by *Tetraoponera penzigi* (Emery), its offspring, and also some coccids. The aperture is found at the tip of what appears to be an aborted limb in the bifurcation of the flowering branch. There

are no swellings and the normal stems are filled with pith. Penzig believes that the ants trim the growing upper end of the branch in order to enter the pith and are thus responsible for the dichotomous inflorescence of this species. I am rather inclined to think that the galleries are bored by some insect larva and are only settled by ants after being left by their maker.

Annibale (1907a) mentions two other African Bignoniaceæ, *Kigelia africana* (Lamarek) and *Newbouldia lævis* (P. de Beauvois), as "myrmecophilous" because he found nectaria on the under side of the leaves. In addition, herbarium specimens of *Newbouldia lævis* examined by him were hollow in the upper part of the flowering branches, the cavities having one or two apertures at the base. The author assumes that these hollows are natural formations of the plant and are settled by the ants, which pierce the exit holes. He does not state that these insects were actually found in the branches, and the explanation offered above for similar cavities in *Stereospermum* is probably also true here.

Grumilea venosa Hiern (Rubiaceæ). Belgian Congo. "Bush of about 2 m., always inhabited by numerous black ants" (Dewevre; see De Wildeman and Durand, 1901, p. 130).

Microdesmis puberula J. D. Hooker (Euphorbiaceæ). Belgian Congo. "Em. Laurent regarded this plant as a myrmecophyte; indeed some of the branches on specimens collected at Bombaie and provided with witch-brooms, are excavated with galleries; but the myrmecophytic character is not much pronounced." (De Wildeman, 1910, 'Études Flore Bas- et Moyen-Congo,' III, 2, p. 250.)

In addition to the ants indicated in the general account of African myrmecophytes which follows, Father Kohl collected at Stanleyville and in nearby localities a number of species "in myrmecophilous plants" which have not been identified thus far in the literature. I subjoin a list of these insects, compiled from Forel's recent paper (1916) on the ants collected in the Belgian Congo by Kohl:

- Crematogaster ruspolti* variety *atriscapis* (Forel).
- C. sjöstedti* subspecies *kohtiella* (Forel).
- C. nigeriensis* variety *wilniger* (Forel).
- C. kasaiensis* (Forel).
- C. kohli* (Forel).
- C. solenopsis* subspecies *flavida* variety *convezictypica* (Forel).
- Monomorium oscaris* subspecies *springalense* variety *paternum* Forel.
- M. exiguum* subspecies *flavescens* Forel.
- Leptothorax evelyna* Forel.
- Tetramorium simillimum* subspecies *ispingense* variety *dumetzi* Forel.

Engramma laurenti variety *congolense* Forel.

Prenolepis grisoni Forel.

Leguminosæ

Though this is one of the four or five largest families of plants and contains many of the more common bushes and trees of the tropics, only very few of its members are known to be myrmecophytes. After the elimination of the East African so-called "ant acacias," which, as I have shown elsewhere, do not possess true myrmecodomatia, there remains in Africa only one genus that possibly presents biocœnotic associations with ants.

SCHOTIA Jacquin

Schotia JACQUIN, 1786, 'Collectanea Austriaca ad Botanicam Chemiam et Historiam Naturalem Spectantia,' I, p. 93. OLIVER, 1871, 'Flora of Tropical Africa,' II, p. 309. HARMS, in Engler and Prantl, 1897, 'Die Natürl. Pflanzenfam.,' Nachtrage zu III, pt. 3, p. 196.

Theodora MEDIKUS, 1786, 'Theodora speciosa, ein neues Pflanzengeschlecht,' p. 16. TAUBERT, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 3, p. 138.

"Unarmed trees or shrubs. Leaves abruptly pinnate, with coriaceous often small leaflets; stipules small. Flowers red or purple, clustered in short often dense panicles, heads or racemes. Bracts and bracteoles caducous or subpersistent. Calyx-tube turbinate, campanulate or narrowly infundibuliform; segments 4, much imbricate. Petals 5, slightly unequal, clawed or subsessile, longer or shorter than the calyx, imbricate. Stamens 10, free or shortly coherent below; anthers uniform, dehiscing longitudinally. Ovary stipitate with elongate style and small terminal stigma; ovules 4 to 8 or 10, or more. Legume oblong, often falcate, compressed, coriaceous, dehiscent or subdehiscent. Seeds exalbuminous" (Oliver, 1871).

This genus belongs to the subfamily Cæsalpinioidæ, in which the flowers are not of the papilionaceous type usual in the family, but possess a rather spreading, zygomorphous corolla; in the bud the upper sepals and petals are covered by the lower. *Schotia* is restricted to tropical and southern Africa and contains twelve species, one of which is supposed to be myrmecophytic.

Schotia africana (Baillon)

Humboldtia africana BAILLON, 1870, 'Histoire des Plantes,' II, p. 99, footnote (Tropical West Africa).

Schotia humboldtioides OLIVER, 1871, 'Flora of Tropical Africa,' II, p. 310. HARMS, 1915, in Engler, 'Die Pflanzenwelt Afrikas,' III, pt. 1, p. 454, fig. 249.

Theodora africana (Baillon) TAUBERT, in Engler and Prantl, 1894, 'Die Natürl. Pflanzenfam.,' III, pt. 3, p. 138.

"A glabrous tree of 25 to 30 feet; extremities (in our specimens) tumid immediately under each node, narrowing gradually nearly to the middle of the internode. Leaves $\frac{1}{2}$ to 1 ft. long, 2- to 4-jugate, glabrous; leaflets thinly coriaceous, the

lowest pair near the base of the leaf, obliquely elliptic-oblong, narrowly acuminate, base very oblique rounded; $4\frac{1}{2}$ to 6 in. long, $1\frac{3}{4}$ to $2\frac{1}{3}$ broad; petiolule 0 to 1 line. Racemes solitary, or 2 or 3 from the axils, $1\frac{1}{2}$ to 2 in. long, densely many-flowered. Bracteoles broadly ovate, about $\frac{1}{2}$ line long. Flowers patent, on pedicels of about 1 line. Calyx $\frac{2}{3}$ to $\frac{3}{4}$ in. long, puberulous or glabrate, the tube but slightly exceeding the limb. Petals oval or ob-lanceolate narrowed at base, slightly longer than calyxlobes. Filaments glabrous, very shortly unequally coherent at the base. Ovary and gynophore pilose; ovules 4 to 5. Legume unknown.

"This plant so much resembles species of the Indian genus *Humboldtia*, that in the 'Genera Plantarum' (of Bentham and Hooker) it is referred to as an African species of that genus. Except in the long narrow calyx-tube and fewer ovules, I do not find any technical character of importance to distinguish it from the other *Schotia*. The minute bracteoles, which persist until flowering, do not enclose the young bud" Oliver, 1871).

Cameroon: River Cameroon (Mann).

According to Harms (1915), who figures the swellings, *Schotia africana* is a tree of the Rain Forest of Cameroon, Spanish Guinea and Gaboon; the internodes of young branches are often swollen towards the upper node and hollow inside. The wall is pierced with a hole through which ants gain access to the inner cavity. This supposed myrmecophyte should be carefully studied in the field. Though having all the appearances of myrmecodomatia, its swellings may still be mere insect galls inhabited by ants after being left by their makers, as is so often the case in the tropics.

Euphorbiaceæ

MACARANGA DuPetit-Thouars

Macaranga DUPETIT-THOUARS, 1806, 'Gen. Nov. Madagascariensia,' p. 26. PAX, 1890, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' III, pt. 5, p. 59. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 932. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 298.

Trees or shrubs. Leaves alternate, petiolate, simple or lobed; their base often palmately and sometimes peltate, occasionally penninerved. Spikes or racemes axillary or lateral or sometimes forming a terminal panicle. Flowers dioecious, rarely monoecious, apetalous. Male flowers small, clustered. Female flowers solitary. Bracts distinct or minute, entire or lobed or fimbriate. Male flower: calyx globose, closed in bud, splitting into 3- to 4-valvate lobes; stamens sometimes few (1 to 3), often numerous (10 to 30); filaments short, free, very rarely united or as if branched; anthers short, terminal, usually 4-celled, 4-valved, sometimes 3-celled, 3-valved, rarely 2-celled; no rudimentary ovary. Female flower: calyx truncate or shortly toothed, ultimately wide-cupular or obliquely spatheaceous; ovary 2- to 3- (rarely 4- to 6-) celled; styles short, stout, entire, free or slightly united at the base, rarely long, slender or united in a globose mass; ovules in each cell solitary. No disk. Capsule breaking up into 2-valved cocci or occasionally, when 1-chambered, almost indehiscent. Seeds globose; testa crustaceous; albumen fleshy; cotyledons broad, flat. (After Prain, 1912.)

The genus *Macaranga* includes over 170 species of trees and shrubs distributed in Africa and its islands, Indomalaya, and the Australian and Polynesian Regions. Some forty species have been described from Tropical and South Africa, fourteen of which are recorded from the Belgian Congo. It is probable that a number of the African species are more or less associated with ants, since several of the Indomalayan forms exhibit various mutualistic relations with these insects. Ridley is even inclined to believe that in some species of this genus symbiosis of the ants and the plant appears to be as complete as possible (see p. 516).

Two of the African species, *M. saccifera* Pax and *M. Schweinfurthii* Pax, have persistent pouch-like stipules which are occasionally occupied by ants. Em. Laurent noticed that in another species, *M. dibeleensis* E. De Wildeman,¹ the leaves attract ants, probably by means of the nectaries at the base of the blade; the stipules are more or less concave, not at all pouch-like, and soon deciduous, so that this species probably is not a true myrmecophyte.

Macaranga saccifera Pax

Macaranga saccifera PAX, 1894, Engler's Bot. Jahrb., XIX, p. 93, Pl. 1. TH. DURAND AND H. SCHINZ, 1896, Mem. Couronnes Ac. Roy. Belgique, LIII, 4, p. 246. E. DE WILDEMAN AND TH. DURAND, 1900, 'Contributions Flore du Congo,' II, p. 57; 1901, 'Reliquie Dewevreana,' p. 212. E. DE WILDEMAN, 1905, 'Mission Emile Laurent,' fasc. 2, p. 130, Pls. XXXIX-XLI; 1908, 'Etudes Flore Bas- et Moyen-Congo,' II, 3, p. 283. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 149. E. DE WILDEMAN, 1910, 'Compagnie Kasai, Miss. Perm. Et. Scient.,' p. 330. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, p. 644, fig. 555. PRAIN, 1912, in Thicketon-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 934. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 312, fig. 51. E. DE WILDEMAN, 1919, C. R. Ac. Sci. Paris, CLXIX, p. 394.

"A shrub or tree; branches armed with spines, densely tawny-pubescent. Leaves long-petiolate, rounded-ovate, deeply 3-lobed; lobes obovate-oblong or triangular, acute; margin repand or toothed; base narrowly deep-cordate; 8 to 10 in. long, nearly as wide, subcoriaceous, gland-dotted beneath, with a pair of marginal glandular processes at the junction with the petiole; petiole 6 in. long; stipules converted into large coriaceous acute flask-shaped sacs. Male flowers in axillary panicles; bracts ovate, acute, subtending several flowers, buds globose. Female flowers unknown" (Prain, 1912).

Pax (1914) distinguishes two forms:

Variety α . *genuina* Pax and K. Hoffmann, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 312, fig. 51.

¹Described by De Wildeman, 1908, in 'Etudes Flore Bas- et Moyen-Congo,' II, pt. 3, p. 281. See also H. Kohl, 1909, p. 150.

"Leaves rather densely glandular underneath. Rachis sparsely pilose; young bracts densely imbricate, almost entire."

French Congo: Libreville (Klaine).

Belgian Congo: Lower Congo: in the Cataract District between Matadi and Leopoldville (Laurent). Kwango: Madibi (Sapin). Kasai: Mukenge (Pogge); Konduc; Batempa; between Lusambo and the Lomami River (Em. and M. Laurent). Upper Congo: Eala (Pynaert; M. Laurent); Bokakata (Dewevre); Bumba (Seret); Injolo (Seret; M. Laurent). Eastern Congo Forest: Patalongo near Yambuya (M. Laurent); Panga (December 19, 1913; J. Bequaert; Coll. No. 1552); in the forest between Walikale and Lubutu (village of Mosekowa, January 21, 1915; J. Bequaert; Coll. No. 6700).

Variety *β. dentifera* Pax and K. Hoffmann, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 313.

"Leaves sparsely glandular underneath. Rachis pubescent; bracts more loosely imbricate, denticulate."

Cameroon: Lomie (village of Bumba); Molundu (Mildbraed).

Macaranga Schweinfurthii Pax

Macaranga Schweinfurthii PAX, 1894, Engler's Bot. Jahrb., XIX, p. 92. TH. DURAND AND H. SCHINZ, 1896, Mem. Couronnes Ac. Roy. Belgique, LIII, 4, p. 246. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 935. PAX, 1914, 'Das Pflanzenreich,' IV, pt. 147, VII, p. 313.

Macaranga rosea PAX, 1899, Engler's Bot. Jahrb., XXVI, p. 328. E. DE WILDEMAN, 1908, 'Études Flore Bas- et Moyen-Congo,' II, 3, p. 283. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 496. PRAIN, 1912, in Thiselton-Dyer, 'Flora of Tropical Africa,' VI, 1, p. 935. MILDBRAED, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 456.

Macaranga Lecomtei BEILLE, 1908, Bull. Soc. Bot. France, LV, Mem., 8, p. 78.

Macaranga calophylla PAX, 1909, Engler's Bot. Jahrb., XLIII, p. 221.¹

"A shrub or tree, sometimes very lofty, reaching 150 feet in height (Chevalier); trunk and branches armed with spines, branches glabrous. Leaves long-petiolate, ovate, shallowly 3-lobed; lobes oblong or triangular, acute; margin irregularly toothed; base narrowly deep-cordate; 6 to 18 in. long, nearly as wide, membranous, becoming firmer with age, gland-dotted beneath, with a pair of glandular processes at the junction with the petiole; petiole 8 to 16 in. long; stipules large, ovate, acute, 1½ in. long. Male flowers in lateral panicles fasciated in the axils of fallen leaves; bracts concave, thick, entire, subtending many flowers. Stamens 2 to 5 (usually 3). Female flowers in short lateral racemes; pedicels short, stout. Sepals ovate, obtuse. Ovary glabrous, 2- to 3-celled; stigmas spreading. Capsule usually 2-coecous; cocci ½ in. across" (Prain, 1912).

French Sudan: Darbanda in the Boro Valley (Chevalier).

Southern Nigeria: Oban (Talbot).

Cameroon: Tibati; Songalong (Ledermann); Bipindi (Zenker); Johann-Albrechtshöhe (Busgen).

¹The synonymy accepted here is from Pax's recent monograph of the Euphorbiaceae (1914).

French Congo: Brazzaville (Chevalier).

Belgian Congo: Upper Congo: Eala (Pynaert); Ikenge (Huyghe). Kasai: Mukenge (Pogge). North-eastern Congo: Beni (Mildbraed); Mangbetu Country at Munza's (Schweinfurth).

Angola: Bamba (Monteiro); Ambriz (Welwitsch).

Anglo-Egyptian Sudan: Niam Niam Country near the river Diangbe and near the river Djur (Schweinfurth).

Uganda: very common (Scott-Elliott; Bagshawe).

Praeger still thinks that *M. rosea* differs from *M. Schweinfurthii* in the shape of the basal sinus of the leaf, which is open in the former and narrow in the latter; Pax (1914), however, believes that both are forms of the same species.

According to Pax (1914), the stipules of *M. Schweinfurthii* are persistent, 3 to 5 cm. long, 2 to 3 cm. broad, slightly saccate at the base, obliquely inserted, acuminate, membranous, glabrous, shortly connate at the base. It is quite possible that, although much less pouch-like than in *M. saccifera*, they may occasionally be occupied by ants, though this has never been observed.

ECOLOGY OF *Macaranga saccifera*

This species is one of the common elements of the undergrowth in the Rain Forest of the Congo, in the eastern district of which I frequently observed it. Growing preferably in low-lying, rather swampy portions of primary forest, it is often found along the banks of rivers or at the edge of brooks. All the specimens I saw were low bushes, rarely over three feet high and generally smaller. Since, however, none of them were in flower or with fruit, they may have been juvenile or dwarfed. The very conspicuous, persistent stipules, placed in pairs at the base of the petiole, are always much swollen, saccate or flask-shaped, about 1 to 3 cm. long, and end in a curved, acuminate apex (Fig. 83). Their texture is more or less coriaceous and hispid hairs are scattered over the outer surface. In each stipule the free, lateral margins are curved close to each other, leaving a very narrow, upper slit as entrance to the pouch. At the foot of the leaf-blade occur two folds, one on either side of the petiole, covering nectaries which I have seen visited by ants. De Wildeman formerly supposed that these folds might shelter mites or even be myrmecodomatia, but I doubt whether such is the case.

That the stipular pouches of *Macaranga saccifera* were occasionally used by ants was merely surmised by Pax on account of the analogy of these organs with similar structures of other myrmecophytes. E. Laurent, however, found ants inside the pouches of the specimens which he collected in the Kasai District, Belgian Congo, and this observation

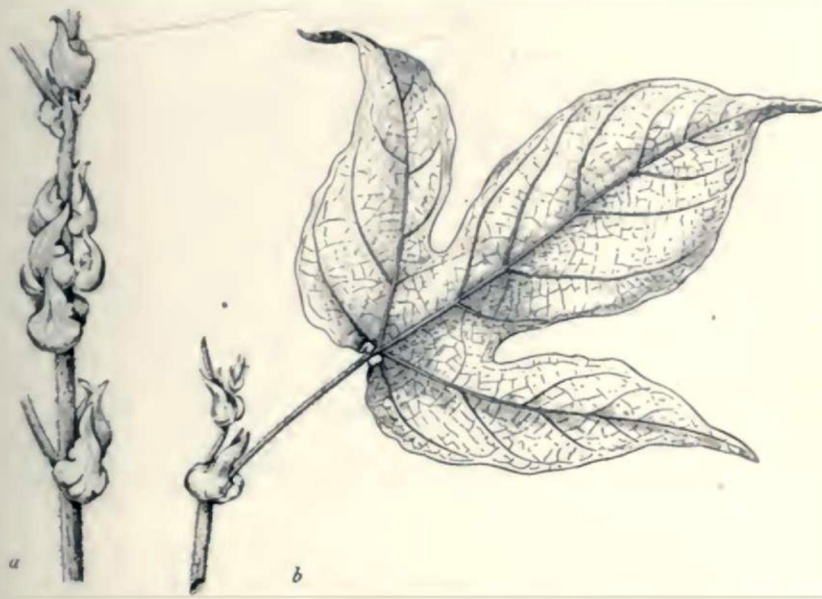


Fig. S3. *Macaranga saccifera* Pax: a, portion of branch with pouch-like stipules; b, extremity of branch with stipules and a leaf seen from above showing the two folds at base of blade. About one-half natural size (after De Wildeman, 1905).

has quite recently been confirmed for my herbarium plants by E. De Wildeman (1919b) who, moreover, points out that *M. saccifera* shelters ants only under certain circumstances. The latter author also mentions that *M. saccifera* has been cultivated for several years at the Brussels Botanical Garden, where it still continues to produce its saccate pouches though these are never utilized by ants.

On only one occasion have I found ants inside the stipular pouches of this plant. Near the village of Mosekowa, between Walikale and Lubutu, in January 1915, a few specimens of *Crematogaster* (*Atopogyne*) *africana* subspecies *tibialis* Santschi occupied some of the stipules. In each case the upper slit leading inside the pouches was not closed with fibres or carton, and no coccids were found with the ants. Since no young or pupae were present, these pouches can not be regarded as the real nest of the ants, but merely as temporary shelters or annexes. In my opinion, this plant belongs to a very primitive stage of myrmecophily, when compared with some of the other African ant-plants. For this very reason, however, its relations to the ants deserve to be more fully investigated.

Sterculiaceæ

COLA Schott and Endlicher

Cola SCHOTT AND ENDLICHER, 1832, 'Meletemata Botanica,' p. 33. MASTERS, 1868, in Oliver, 'Flora of Tropical Africa,' I, p. 220. K. SCHUMANN, 1895, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 6, p. 99; 1900, 'Sterculiaceæ Africanae,' in Engler, 'Monogr. Afrik. Pflanzenfam.,' V, p. 110.¹

Educardia RAFINESQUE, 1814, Specchio delle Scienze, Palermo, I, p. 158 (not *Educardia* Salisbury, 1808).

Lunanea A. DE CANDOLLE, 1825, 'Prodromus Regn. Veget.,' II, p. 92.

Trees, shrubs or bushes. Leaves entire or lobed, often polymorph, rarely digitate; glabrous, hairy or scaly. Flowers in axillary panicles or clusters, sometimes out of the old wood. Flowers through abortion unisexual or polygamous. Calyx cup-shaped or campanulate, 4- or 5-cleft. Petals absent. Staminal column sometimes very short, bearing at the top a ring of 10 to 12 anthers, disposed in one or two, regular rows; anther-cells (thecae) parallel or superposed. Ovary 3- to 10-celled, with as many styles as cells. Ovules numerous in each cell. Fruit of 4 or 5 leathery or woody oblong carpels, ultimately splitting lengthwise. Seeds numerous, obovoid, exalbuminous; cotyledons thick, sometimes deeply bifid; radicle next to the hilum. (After K. Schumann.)

This large genus is restricted to the continental part of the Ethiopian Region. About one hundred species have been described, most of which grow in that portion of Africa defined by Engler as the "Western Forest Province" and twenty-five of them occur in the Belgian Congo. A few very closely allied forms possess at the base of the leaf-blade a pair of small pouches which are occasionally inhabited by ants. In addition, these myrmecophilous species differ from their relatives in having branches and leaves covered with numerous long, stiff, erect hairs of a brown or brownish red color; the other members of the genus being glabrous.

Cola Dewevrei De Wildeman and Durand

Cola Dewevrei E. DE WILDEMAN AND TH. DURAND, 1899, Bull. Soc. Bot. Belgique, XXXVIII, 2, p. 184; 1901, 'Reliquia Dewevreana,' p. 24. E. DE WILDEMAN, 1907, 'Mission Emile Laurent,' fasc. 4, p. 406, Pl. CXXVII. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 62. E. DE WILDEMAN, 1920, 'Mission de Briey au Mayumbe,' p. 191.

"A low shrub, 1 to 2 m. high. Branches hollow, terete, with long pilosity. Leaves trilobate, deeply cordate at the base, abruptly acuminate at the apex, shiny on upper and under sides, pilose, especially on the veins. Secondary veins arcuately anastomosing toward the margin and uniting with the reticulate finer venation, a little prominent above, more strongly so below. Petiole very long, more or less grooved above, with long pilosity, 6 to 32 cm. long. Leaves 13 to 25 cm. long and 15 to 24 cm. broad. Stipules linear-lanceolate, dropping, pilose, about 6 to 11 mm. long and 1 to 1.5 mm. broad. Flowers yellow, fasciculate, axillary, subsessile, bracteate. Calyx

¹According to the rules of botanical nomenclature the name *Cola* should be replaced, it seems, either by *Educardia* or by *Lunanea*, since the latter two are not preoccupied and evidently have priority.

5-lobed, ferruginous tomentose externally, brown and less pilose inside, about 11 mm. long; its lobes 2 to 3 mm. long, acute, with more or less reflexed tips. Androecium of the male flowers stipitate, smaller than the calyx, with subglabrous stipe, 4 mm. long; the anthers placed close together, parallel and united into a ring which is about 15 mm. high" (De Wildeman and Durand, 1899).

Belgian Congo: Mayombe: Lemba River (Dewèvre).

It would seem from the descriptions that the later *C. Laurentii* De Wildeman and the earlier *C. marsupium* K. Schumann are not specifically distinct from *C. Dewevrei*. According to De Wildeman (1907, p. 406), the leaves of *C. Dewevrei* have a different shape from those of *C. Laurentii*, with basal lobes almost touching each other. In these *Colæ*, however, the form of the leaves varies to such an extent even on the same plant that this character is by itself unsatisfactory for the distinction of the species. The existence of foliar pouches is not mentioned in the original description of *C. Dewevrei*, but De Wildeman's figures of that species published in 1907 show them distinctly.

Cola Laurentii De Wildeman

Cola Laurentii E. DE WILDEMAN, 1907, 'Mission Emile Laurent,' fasc. 4, p. 403, fig. 68, Pls. cxxxv, cxxxvi, and cxxxvii; 1908, 'Etudes Flore Bas- et Moyen-Congo,' II, 3, p. 304. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 63. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 148. A. ENGLER, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 506. E. DE WILDEMAN, 1919, Bull. Jard. Bot. Bruxelles, V, p. 358.

"A small tree with cylindric branches densely villose; with brownish, elongate, spreading hairs which drop late. Leaves with more or less lengthened petioles, which are cylindrical, hispid with spreading hairs, 5 to 35 cm. long. Leaf-blade 3-lobed or nearly 5-lobed, cordate at the base; the midlobe about two thirds the length of the leaf, which varies from 11 to 36 cm.; the midlobe is oblong, rather suddenly acuminate at the tip, acute; lateral lobes about of the same shape, a little shorter and narrower than the terminal lobe, which reaches a length of 23 cm. and a width of 13.5 cm. Leaf-blade paler on the under than the upper side or about the same color, with 7 basal veins, the lateral ones often united at the base. Leaf-blade coriaceous, glabrous, except on the veins of both sides, especially on those of the under side which are very prominent and bristling with stiff hairs. Between the midrib and the first lateral vein on each side of it there is a small pouch strongly projecting on the upper side; the two veins between which this pouch is formed are united at the base by a plate of tissue. Stipules filiform, hispid, rather dropping, about 2 cm. long, acute. Flowers fasciculate at the axils of the leaves; the rachis about 1 cm. long; the bracts linear, acuminate, hispid, about 2 mm. long; the pedicels villose, a little over 1 mm. long. Calyx campanulate, about 8 mm. long; with 4 to 5 lobes one-third the length of the tube; calyx densely villose, brownish on the outer side, with more scattered hairs internally. Male flowers with an uniseriate androecium, composed of three a little over 2 mm. long, borne on a slender, feebly elevated androgynophore which is 3 to 4

mm. long and shorter than the calyx-tube. Female flower with a densely villose, ovoid ovary; the style shorter than the ovary, with spreading stigmata which are as long as the calyx-tube. Staminodes reduced, surrounding the base of the ovary. Fruits red, 5 to 6 cm. long including the acumen, with 4 to 5 seeds" (De Wildeman, 1907).

Belgian Congo: Lower Congo: Sabuka (M. Laurent); between Boma and Yanga (R. Verschueren). Kasai: Dibebe; Kondue (Em. and M. Laurent); forest of the Sankuru (Laja). Upper Congo: Eala; Yakusu (Em. and M. Laurent); Yambinga (M. Laurent); Dundusana (F. Reygaert); Barumbu (November 3, 1913; J. Bequaert; Coll. No. 1081). Eastern Congo Forest: Yambuya (M. Laurent); Basoko (Em. and M. Laurent); Fariala between Mawambi and Avakubi (*f. integrifolia*; Mildbraed); between Lubutu and Kirundu (village of Uchibango, February 1, 1915; J. Bequaert; Coll. No. 6790); Stanleyville (March 1915; H. Lang).

De Wildeman classified as "form *intermedia*" plants of this species in which entire and trilobed leaves are found on the same branch together with all intermediate shapes; his "form *integrifolia*" includes specimens in which all the leaves are entire, ovate-cordate at the base and as much as 35 cm. long and 18 cm. broad; in this last form pouches are also feebly developed along the midrib in the axils of the first or first and second lateral veins, above the large basal pouches.

In recording the form *integrifolia*, Engler (1912, p. 506) also mentions that in his opinion *C. Laurentii* is not specifically distinct from *C. marsupium*.

Cola marsupium K. Schumann

Cola marsupium K. SCHUMANN, 1891, Ber. Deutsch. Bot. Ges., IX, pp. 68-70; 1900, 'Sterculiaceae Africae,' in Engler, 'Monogr. Afrik. Pflanzenfam.,' V, p. 113, Pl. XII, figs. A-D. H. Kuntz, 1909, Natur u. Offenbarung, LV, p. 148.

"A shrub or tree, with slender, terete branches, the younger ones flattened and strongly hispid, later glabrescent. Leaves with long, terete, hispid petioles; oblong or obovate-oblong, shortly and very sharply acuminate, cordate at the base; with 7 or even 9 veins; provided with a pair of pouches forming basal swollen domatia between the midrib and the lateral veins; covered with rather long hairs on the veins on both sides, rather rigidly herbaceous. Stipules filiform, hispid, persistent for a long time. Flowers short pedicellate, axillary, fasciculate, placed either at the extremity of branches which are rather sparsely leaved below or on leafless branches. Bracts and bracteoles linear, acuminate, hispid. Calyx campanulate; its upper third split into 4 or 5 ovate, acute lobes; tomentose outside, papillate inside. Male flower: androecium uniseriate of 16 to 20 thecae, raised on a gracile, glabrous column. Female flower: ovary subglobose, pentamerous, tomentose; the style glabrous, straight, 5-lobed; 8 ovules in each cell; follicles short stipitate, fusiform.

"The shrub reaches a height of 1 to 2.5 m.; the tree as much as 10 m. The foliate, flowering branches are 3 to 3.5 mm. thick at the base and 20 to 25 cm. long; they are rough, being covered with simple, spreading, brown red or brown hairs, which are thickened into a tubercle at the base. The petiole is 1.5 to 15 cm. long and covered with the same pile. The blade has a length of 6 to 30 cm. and a width of 3 to 13 cm.

above the middle; in addition to the basal veins, it is crossed on each side of the midrib by only 5 to 6 stronger veins, which are a little more prominent on the under side, as is also the reticulate venation; sometimes the blade is somewhat gibbous; in life it is dark green, brownish green when dry. The basal pouches can be entered from the under side; they are not always present, but usually found on the larger leaves. The stipules are 1 to 1.5 cm. long and covered with brown hair. The bracts of the flowers are usually somewhat broader than the stipules, but otherwise similar. The yellowish green calyx is 5 to 7 mm. long. Male flower: androecium 1.5 mm. long, as well as the androgynophore. Female flower: calyx slightly larger; ovary 6.5 mm. long, surrounded at the base by a ring of staminodes 2 mm. high. The fruit is red, but perhaps not entirely ripe" (K. Schumann, 1900).

Cameroon: Abo (Buchholz); Johann-Albrechtshöhe: in the Senge Mountains (Staudt).

French Congo: Maveli Mountains near the Sibange Farm (Dinklage).

It seems probable that the three forms described above, *C. Dewevrei*, *C. Laurentii*, and *C. marsupium*, all belong to one species, for which the name *C. marsupium* K. Schumann should be retained. This is, however, a question to be decided by botanists and, in order to avoid any possible confusion, I have here used the name *C. Laurentii* for the plants observed by me in the Belgian Congo, because the description of that species fits them most nearly.

ECOLOGY OF *Cola Laurentii*

This plant is rather common in the Congo Basin, where it prefers the drier, more elevated parts of the primitive Rain Forest. It usually grows as a shrub of moderate size (1 to 2.5 m. high), more rarely as a small tree (as much as 10 m. high) and flowers in both forms. The leaves are, as mentioned above, of variable size and shape, usually elongate-oval, with cordate base; the margin may be entire, or slightly or deeply lobate. The pair of basal, elongate-oval pouches on the leaves are more or less developed; wholly absent in certain cases, in others they may attain 15 mm. in length and 5 mm. in width; on the average they are 4.5 to 9 mm. long, 1.5 to 4 mm. broad and 6 mm. high. Placed at the base of the blade close to the midrib, they project on the upper side of the leaf and on the under side have a narrow slit their entire length.

The general aspect of *C. Laurentii* is illustrated on Plate XXVII, Figure 2, by a photograph of a branch, with flowers and fruit, made by Mr. H. Lang at Stanleyville, while the shape of the myrmecodomatia is seen in Text Figure 84. As mentioned by Em. Laurent (De Wildeman, 1907, p. 405), the pouches are only occasionally occupied by ants. They were empty on most of the many plants which I examined. On one occasion, near the village of Uchibango, between Lubutu and Kirundu (February 1915), ants belonging to the dolichoderine *Engramma kohli*

Forel were found inside the pouches; they had closed the slit at the under side with vegetable detritus. Unidentified ants were also found in such swellings at Barumbu (November 1913). Some of the plants collected by Mr. H. Lang along the Tshopo River near Stanleyville, in March 1915, were inhabited by *Plagiolepis mediorufa* (Forel), an ant originally described from specimens taken by Father Kohl in a nearby locality from an unidentified myrmecophilous plant. *Engramma kohli*,

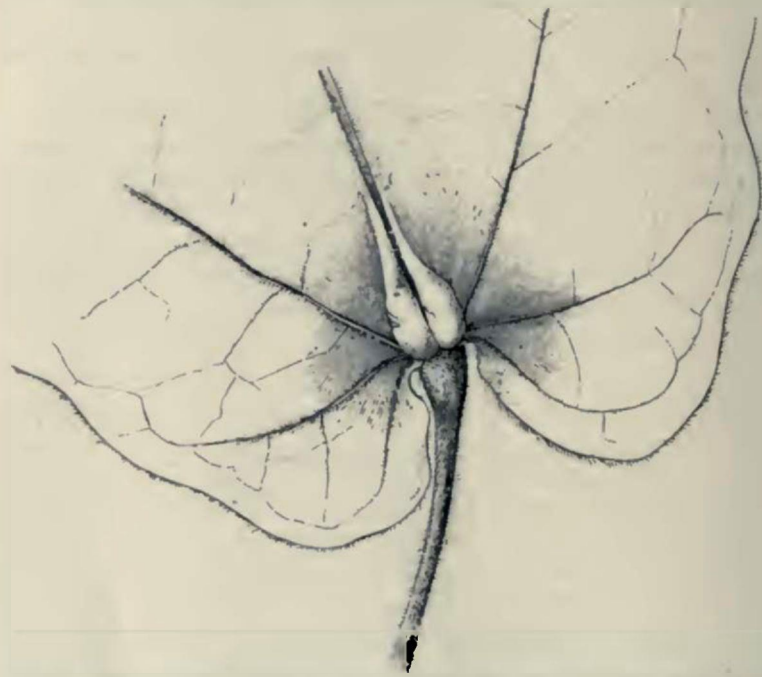


Fig. 84. *Cola Laurentii* De Wildeman. Lower part of a leaf seen from above, with the two pouches at base of blade. Drawn from life at Barumbu, November 1913. About natural size.

like certain other members of the genus, is a frequent inhabitant of various myrmecophytes. Both *Engramma* and *Plagiolepis* are so timid and small that they could not well act as body-guards to their host plant.

Although K. Schumann (1891, pp. 68-70) describes the ascidia of *Cola marsupium* very fully and regards them as myrmecodomatia, he was unable to find ants on his herbarium specimens from Gaboon and Cameroon. H. Kohl (1909, p. 148) is inclined to believe that, on account of the small size, these pouches are not adapted to the use of ants but serve better as shelters for coccids or plant lice.

SCAPHOPETALUM Masters

Scaphopetalum MASTERS, 1867, Journ. Linn. Soc. London, Botany, X, p. 27; 1868, in Oliver, 'Flora of Tropical Africa,' I, p. 236. K. SCHUMANN, 1895, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' III, pt. 6, p. 86; 1900, 'Sterculiaceæ Africane,' in Engler, 'Monogr. Afrik. Pflanzenfam.,' V, p. 90.

Shrubs with petiolate, oblong, entire, unicostate, glabrous leaves. Flowers yellow or yellowish-green, pedunculate, placed in cymes or clusters, axillary or emerging from the trunk or older branches. Calyx of 5 valvate sepals, more or less coherent, sometimes forming a 2-valved calyx. Petals 5, hooded, nervose-striate, without appendages or laminae. Filaments united into an angular, funnel-shaped, membranous tube, which bears at the upper margin 5 roundish reflexed staminodes alternating with the sepals; anthers in phalanges of 3 between the staminodes, more or less concealed within the concavity of the petals, 2-lobed and 5-celled; ovules either numerous, arranged in two rows on the inner angle of each cell, or few, two or four above one another in one or two rows. Styles connate. Stigma obsolete 5-lobed, capitate. Fruit a capsule with feebly fleshy walls, loculicidal. Seed, as far as known, with a curled arillus. Cotyledons flattened, foliaceous in the albumen.

This small genus contains eight described species and is peculiar to the Western Forest Province of the Ethiopian Region, from Cameroon and Gaboon to the Upper Congo. The two myrmecophytic species are the only members of the genus which have thus far been recorded from the Belgian Congo. They have been placed by K. Schumann in a section of their own, whose characters are as follows.

Section *Physcophyllum* K. Schumann. Ovules few in number, from 2 to 4 in each cell of the ovary, placed in one or two rows. Upper side of the leaves with an elongate, spindle-shaped pouch at the base of the blade on one side of the midrib. Flowers small; calyx-lobes with soft hair (after De Wildeman and Durand).

Contains only two species which have been separated thus:

Leaves oblong-lanceolate. Fruit not as high as broad, with 5 very distinct cells, which are rounded at the back and end in a pointed tip; two seeds in each cell.

S. Thonneri De Wildeman and Durand.

Leaves obovate, narrowed towards the base. Fruit higher than broad, with 5 very distinct cells, which are subangulate at the back and taper gradually towards an erect, feebly pointed apex; four seeds in each cell.

S. Deweyrei De Wildeman and Durand.

Scaphopetalum Deweyrei De Wildeman and Durand

Scaphopetalum Deweyrei E. DE WILDEMAN AND TH. DURAND, 1901, Bull. Soc. Bot. Belgique, XXXIX, 2, p. 97; 1901, 'Reliquie Deweyreane,' p. 26. E. DE WILDEMAN, 1905, 'Études Flore Bas- et Moyen-Congo,' I, p. 167. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 66. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 111.

Scaphopetalum Thonneri E. DE WILDEMAN AND TH. DURAND, 1898, 'Illustrations Flore du Congo,' I, pp. 13-14 (*pro parte*). Pl. VII; 1900, 'Planta Thonnerianæ Congolenses,' p. 26 (*pro parte*). Pl. XIX.

"Shrub about 2 m. high, covered with brown pile towards the apex of the branches, the stem otherwise glabrous. Leaves alternate, obovate, subcordate at the base, abruptly and sharply acuminate at the apex, entire; greenish-gray above, greenish-brown below, subcoriaceous, not shiny above; glabrous or sparsely pilose near the veins; 14 to 20 cm. long, 4.5 to 6.5 cm. broad beneath the apex, about 2 cm. broad near the base; petiolate, the petiole 5 to 6 mm. long, thick, silky. Leaves asymmetric, unilaterally constricted towards the base, which bears on the upper side a small pouch acuminate towards its tip and opening below in the axil of the penultimate lateral vein. On each side of the midrib there are about 8 lateral veins, projecting slightly on the upper, more strongly on the under side and arcuately anastomosing before the margin; a conspicuous, dense network of anastomosing venules. The basal lateral vein and the midrib nearly meet on one side of the leaf, and unite by a secondary vein, enclosing thus the opening of the pouch. Stipules subulate, more or less persisting, 5 to 12 mm. long, fasciculate, each cluster 10 to 20 mm. long, branched, axillary, pedicellate, the pedicel 5 to 7 mm. long, bracteate; the bracts subulate, ciliate. Sepals 5, free almost to the base, oblong, velutinous externally, more or less keeled, with three veins. Petals 5, subequal with the sepals, oblong, with recurved apex, hood-shaped, longitudinally striate. Tube of the stamens membranous, pentagonal, salver-shaped, with 5 fertile edges, the intervening lobes sterile; the fertile lobes opposite the petals. Petals covering the stamens in the bud; there six for each phalange; the three subsessile; sterile lobes briefly tridentate, the median tooth obtuse, the lateral teeth narrow. Ovary oblong, 5-celled. Style entire, erect or slightly curved at the apex. Fruit red, stellate, 7 mm. long and about 3.5 mm. broad, with a prominent, horned apex; it is divided into 5 distinct cells, each of which contains 4 seeds, inserted on a central placenta.

"Differs from *S. Thonneri* in the leaves and fruit, and in the number of ovules or seeds contained in each of the cells of the ovary or fruit" (De Wildeman and Durand, 1901).

Belgian Congo: Eastern Congo Forest: forest at Matchacha (Dewèvre).¹ Kasai: Konduc (Luja).

Dewèvre wrote the following field-notes for his specimens: "calyx green; corolla orange-yellow with red stripes; coronula (or stamens-tube) with red edges; anthers brown; the leaves have at the base a fold inhabited by numerous red-brown ants with black abdomen." Luja found *Engramma lujæ* Forel in the pouches of *S. Dewèvrei* at Konduc.

Scaphopetalum Thonneri De Wildeman and Durand

Scaphopetalum Thonneri E. DE WILDEMAN AND TH. DURAND, 1897, Bulletin de l'Herbier Boissier, V, June, p. 521, Pl. XXI; 1901, Bull. Soc. Bot. Belgique, XXXIX, 2, p. 96. E. DE WILDEMAN, 1907, 'Mission Emile Laurent,' fasc. 4, pp. 400-402, figs. 66 and 67, Pls. cxli and cxlii; 1907, *ibid.*, fasc. 5, p. cxxxiv, fig. xii. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 66. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 110, Pl. 1. A. ENGLER, 1912, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 503. E. DE WILDEMAN, 1919, Bull. Jard. Bot. Bruxelles, V, p. 356.

¹To judge from Dewèvre's itinerary, this locality is situated on the banks of the Congo River (Lualaba) between Ponthierville and Nyangwe; I have not found it on any map.

Scaphopetalum monophysea K. SCHUMANN, 1897, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' Nachträge z. I-IV, October, p. 247, without description; 1900, 'Sterculiaceae Africanae,' in Engler, 'Monogr. Afrik. Pflanzenfam.,' V, p. 93, Pl. VII, Fig. A, a-t.

"Shrub, 2 m. high. Petioles short, 6 to 8 mm. long, villose, shorter than the stipules. Stipules subulate, with well-marked, parallel veins, sometimes deciduous. Extremities of the branches covered with erect brown hairs. Leaves alternate, oblong, acuminate, entire, green, shiny on the upper face, coriaceous, glabrous except along the midrib on the upper face, where the pilosity of the petiole extends upwards, but is less distinct. Leaves 9 to 23 cm. long, 2.5 to 7.5 cm. wide, narrowed towards the base, asymmetric; the right half of the leaves placed on the right side of the branch, and the left half on the left side. Lateral veins pinnate. Upper face of the leaves showing on the narrowest half a basal pouch-shaped fold which opens on the under side near the midrib. Veins of the under side asymmetric; the first lateral vein on either the right or the left half, instead of leaving the midrib almost at a right angle, makes a very acute angle and, at 20 to 25 mm. from its base, unites with the second lateral vein close to the midrib by means of a veinlet. The opening of the pouch is placed between the midrib and this first lateral vein, and is thus not a pore. Flowers small, about 5 mm. long, in branched, more or less dichotomous clusters which are erect, 10 to 20 mm. long, and inserted in the axils of leaves, which usually hide them, the leaves often covering part of the branch with their broadened base. Flower peduncles 5 to 6 mm. long, with small, subulate bracts. Buds elliptic-ovoidal, with 5 distinct ribs ending at the apex in obtuse tips and narrowing towards the base. Sepals 5, free almost to the base, oblong, villose externally, more or less keeled, with 3 well-marked veins. Petals 5, green, about as long as the sepals, oblong, obtuse, recurved and hood-shaped towards their apex, distinctly striate. Tube of the stamens membranous, pentagonal, divided into 10 segments; the 5 edges are fertile, the intermediate segments sterile. Fertile lobes covered in the bud by the petals, bearing outside the apex 6 thecae. Sterile lobes somewhat recurved towards the apex and with a small horn on each side of their median portion, near the anthers. Ovary oblong, with 5 feebly marked lobes, 5-celled. Style simple, straight or feebly recurved towards the apex. Fruit red" (De Wildeman and Durand, 1897).

Additional characters of importance are found in the fruit, which in this species is about 1 cm. long and distinctly broader than high; its 5 lobes are rounded on the back and distinctly apiculate at the apex; each of the 5 cells contains two seeds.

Cameroon: Bipindi; Undua (Zenker); Lolodorf (Staudt); between Kribi and Ngumba (Dinklage).

Belgian Congo: Upper Congo: Bobi near Gali, type locality (Thonner); Kapinga; Ibaka; Yakusu (Emile Laurent); Barumbu (November 1, 1913; J. Bequaert; Coll. No. 1078); Dundusuna (Mortehau); Mobwasa (H. Lemaire). Eastern Congo Forest: Yambuya (November 26, 1913; J. Bequaert); Avakubi (January 1, 1914; J. Bequaert; Coll. No. 1919); Niapu (Lang and Chapin); Ihulu between Mawambi and Irumu (Mildbraed); near Walikale (January 1915; J. Bequaert); Mission St. Gabriel near Stanleyville (H. Kohl); Lesse (June 15, 1914; J. Bequaert; Coll. No. 4773).

All the specimens I have seen in the Belgian Congo agreed with the descriptions of *S. Thonneri*. It must, however, be noted that the shape and size of the leaves are extremely variable; it is not rare to see them a

length of 30 to 40 cm. and a width of 12 to 15 cm.; they may be gradually tapering at the apex, abruptly constricted into an acumen, or even sub-obtuse.

ECOLOGY OF Scaphopetalum Thonneri

This species is in many places a common bush of the undergrowth in the primitive, rather dry, and often very shady Rain Forest. Its stems are irregularly branched and never grow very high, usually reaching 1 to 2 m., more rarely as much as 4 m. The young branches are densely covered with stiff, erect, brownish-red hairs, a peculiarity which is often found among myrmecophytes, though far from being the rule. While I have observed this plant in many places and at various seasons, I have but seldom seen it with flowers. These are inconspicuous, yellowish green, with the petals carmine red on the inner side.

The peculiar pouch at the base of the leaf-blade is shown on Plate XXVII, Figure 1, from a photograph taken by Mr. Lang. Such an ascidium is present on all the leaves of the plant, though its size is variable. As a rule, it consists of a very elongate, club-shaped evagination of the blade on the upper side, laterally near the midrib, and opens on the under side by a narrow slit its entire length. This pouch may be 25 to 50 mm. long and is very narrow in the distal half or two-thirds; nearer the base of the leaf it swells rather suddenly and reaches a width of 6 to 8 mm. The slit on the lower surface of the pouch is placed between the midrib and the first lateral vein, which, on that side of the leaf, is deflected from its normal, oblique course and runs close to and parallel with the midrib the whole length of the slit. Furthermore, at the distal end of the opening the deflected lateral vein is connected with the midrib by means of a short cross-vein. As a result of this peculiar structure, the base of the leaf becomes asymmetric, the pouch-bearing side being usually much narrower and tapering more gradually towards the petiole, while the opposite side expands into a broad, semi-cordate lobe which covers the branch. The leaves are apparently arranged alternately in two rows and are more or less horizontal, nearly in one plane. When a branch is seen from above with the extremity farthest from the observer, all the leaves to the right have the pouch on their right half, while those to the left have the pouch on the left half. This arrangement of the leaves and ascidia, more or less distichous in appearance, is well illustrated on the plate.

In most cases the pouches of this plant are empty, but on two occasions, at Barumbu and Yambuya, in November 1913, I found unidentified ants in them. These insects had established regular formicaries

therein, with a queen, larvæ, and pupæ, and had even brought coccids into the cavities; furthermore, they had closed the slit almost completely with a tent of brownish vegetable fibres. At Niapu, in January 1914, Mr. H. Lang collected two species of *Engramma*, *E. kohli* Forel and *E. lujæ* Forel, from the ascidia of this *Scaphopetalum*. So far as recorded, the ants which inhabit these pouches are small and timid; they do not emerge from their retreats when the plant is disturbed and contribute little or nothing to the protection of their host. The leaves of *Scaphopetalum Thonneri* are frequently injured by phytophagous insects, even when their pouches are occupied by ants.

While drawing up the original description, De Wildeman and Durand found a few ants in the pouches of the specimens collected by Thonner and thus recognized the myrmecophily of this species. Emile Laurent's short field-notes are to be found in the account of the plants he collected (De Wildeman, 1907).

Flacourtiaceæ

Only one genus of this family, *Barteria*, is definitely known to contain true myrmecophytes. Certain species of other genera have been found in association with ants, but there is reason to believe that they had been settled only by accident. The best-known of these is the African *Buchnerodendron speciosum* Guerke,¹ a common bush or small tree of the primary Rain Forest, also found in forest galleries along streams in the Savannah. On a specimen observed at Romée, near Stanleyville, H. Kohl (1909, pp. 109-110) found that "the branches, 1 m. in length, were all hollow to within 5 cm. of their tips and inhabited by small black ants, *Crematogaster excisa* Mayr.² Two or three apertures led into the cavity. I did not find coccids on the inner walls of these branches, several of which I cut open, though such were seen in the axils of the leaves where they were actively attended by the ants." Kohl, however, believes that this plant was only accidentally occupied by ants, an opinion with which I am in complete agreement. I have repeatedly found this *Buchnerodendron* growing under a variety of conditions and, though my attention was especially directed to its possible relations with ants, I never saw any of these insects inside its branches.

¹Described in Engler's Bot. Jahrb., XVIII, 1894, p. 161, Pl. iv.
²Forel (1909b, p. 69 and 1910, p. 408) identified this ant found by Kohl inside *Buchnerodendron speciosum* as *Crematogaster impressa* Mayr.

In the original description of *Caloncoba Laurentii* (De Wildeman and Durand)¹ the branches of this tree are said to be fistulose and the following notes are given: "*C. Laurentii* is myrmecophilous; the stem is hollow for a long distance and pierced with exit holes at various levels, either at the cicatrice of a leaf base or at any other point along the internode. There were several ants inside the specimens we saw." Gilg, who, it seems, examined some of the type material, did not find the stems hollow nor pierced with orifices, and concluded that one of the branches had been accidentally settled by ants, probably in a former burrow of some wood-boring larva.

BARTERIA J. D. Hooker

Barteria J. D. HOOKER, 1860, Journ. Linn. Soc. London, Botany, V, p. 14. MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' V, p. 510.

Tree or shrubs, rarely over 20 m. high, usually much lower, with thick, horizontal branches. Leaves large, leathery, alternate, oblong or oval, subacuminate, almost entire, with short, thickened petioles. No stipules, the decurring base of the leaf forming a raised line on both sides of the stem. Flowers dichlamydeous, hermaphrodite, subsessile, arranged in dense axillary or supra-axillary tufts or rows, rarely solitary; surrounded by overlapping bracts which completely enclose the flower-bud. Calyx-tube short, deeply divided into 5 oblong-lanceolate, overlapping, white sepals, which are silky at the outer side. Petals 5, inserted on the inner edge of the calyx-tube, similar to the sepals, white. Corona duplicate, emerging from the throat of the calyx-tube; outer row membranous, jagged at the edge, about half the length of the petals; inner row much smaller, consisting of a ring of thick, fleshy tubercles. Stamens numerous, monadelphous at the base, emerging from the base of the calyx-tube; filaments in two rows; anthers linear-oblong, introrse. Ovary sessile, globose, surmounted by a single, thick style, which terminates in a large, mushroom-shaped stigma. Ovules numerous, inserted on 3 or 4 parietal placentas. Fruit a coriaceous, ovoid, indehiscent berry; seeds ovoid, compressed, with a crustaceous, coarsely pitted testa.

The genotype, *B. nigritana* J. D. Hooker, was discovered by Barter at the mouth of the Niger, during the Baikie Niger Expedition (1859). The genus is strictly Ethiopian with a small number of species peculiar to the Rain Forest and extending but little beyond it into the forest galleries of the neighboring grass-lands. The area of its distribution, indicated by the interrupted line on Map 19, falls entirely within the limits of the "Western Forest Province" as defined by Engler. That *Barteria* is thus far unknown from the forests of Upper Guinea, west of

¹'Contributions Flore du Congo,' I, 1899, p. 8 (Coquilhatville). According to Gilg (Engler's Bot. Jahrb., XL, 1908, p. 463), this is merely a synonym of *Caloncoba Welwitschii* (Oliver), a common bush or low tree in the forests of Cameroon, Gaboon, Belgian Congo, and Angola. The synonymy of *C. Laurentii* and *C. Welwitschii* is accepted by Th. and H. Durand in their 'Sylloge Floræ Congolanae,' 1909, p. 37. I have very often observed *C. Welwitschii* and never seen it associated with ants.

Nigeria, is remarkable, and can hardly be ascribed to insufficient investigation. Nor has its guest ant, *Pachysima*, been recorded there, which is interesting in view of the fact that Map 19 shows the known distribution of the two species of that ant genus to be included within the area occupied by *Barteria*. This genus of pseudomyrmecine ants is, indeed, almost restricted to the hollow stems and swellings of various *Barteria*, its only other known habitat being the caulinary swellings of *Epitaberna myrmecia* in Cameroon (Stitz, 1910, p. 131; see p. 442). It would not be amiss to ascertain whether the *Barteria* of Uganda are also inhabited by these ants.

The species of *Barteria* are, together with those of *Scaphopetalum*, the commonest and most widely distributed of African myrmecophytes. They are erect bushes or small trees with a very characteristic habitus. Either all the branches are uniformly hollow throughout or some of them have hollow swellings at their base. The flowers are large and showy, with white calyx and corolla, numerous stamens and a single, entire style ending in a mushroom-shaped stigma; they are enclosed in overlapping bracts and placed in oblique rows, in loose tufts, or singly, in the axils of the leaf or along the decurrent leaf-bases.

There are undoubtedly a number of different species in the genus; but how many is hard to say at present, since the published diagnoses are so incomplete as hardly to permit the correct identification of specimens. Gilg (1908) recognizes four species in his recent revision of African Flacourtiaceæ, but he has evidently overlooked the description of *B. acuminata* E. G. Baker, which is possibly identical with *B. Stuhlmannii* Gilg.

Barteria acuminata Baker

Barteria acuminata E. G. BAKER, 1905, Journ. Linn. Soc. London, Botany, XXXVII, p. 155.

"Low tree or bush. Branches striate, with fine rufous pubescence, or later on glabrate. Leaves oblong or oblong-elliptic, coriaceous, almost glabrous, acuminate at the apex, attenuate at the base into the petiole. Petiole very short, thick, not stipulate, decurrent. Leaf-blade with about 16 to 19 lateral veins visible on both sides and uniting arcuately before the margin; also with a reticulate venation rather prominent on the upper face. Flowers: 1 or 2 in the axils, sessile, bracteate at the base; the bracts numerous, closely imbricate, cupuliform, brown, shiny, ciliate along the margin. Sepals 5, ovate-oblong, acuminate, longer than the petals, coalescent at the base. Petals white, oblong, mucronate at the apex. Stamens numerous. Stigma very large, conical-globose, yellow. Fruit globose.

"Species related to *B. nigritana* Hook. fil., but differing in the leaves being gradually acuminate at the apex.

"Leaves 22 to 24 cm. long, 6 to 7 cm. broad. Petiole about 6 to 8 mm. long, canaliculate above. Sepals 2.8 to 3 cm. long, 10 to 11 mm. broad. Anthers about 3 mm. long" (E. G. Baker, 1905).

Uganda: Musozi on the shore of Lake Victoria, type locality (Bagshawe). This is very close to Bukoba, the type locality of *B. Stuhlmannii* which perhaps is merely a synonym of *B. acuminata*.

Barteria Dewevrei De Wildeman and Durand

Barteria Dewevrei E. DE WILDEMAN AND TH. DURAND, 1899, 'Contributions Flore du Congo,' I, p. 8; 1901, 'Reliquiae Dewevreanae,' p. 97. E. DE WILDEMAN, 1906, 'Mission Emile Laurent,' fasc. 3, pp. 217-219, Pl. xxxii; 1908, 'Études Flore Bas-et-Moyen-Congo,' II, p. 316. GILG, 1908, Engler's Bot. Jahrb., XI, p. 480. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 108. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 223.

"Tree 5 to 6 m. high, branched, glabrous. Leaves oblong-elliptic, green above, paler underneath, brown when dried, acuminate, attenuate at the base into the petiole, which is very short, thick, blackish, not stipulate, decurrent; the blade 27 to 34 cm. long and about 11 cm. broad; with about 14 nerves below and above on each side, uniting before the margin; the under side with a feebly prominent, reticulate nervation. Flowers 2 to 4 together, axillary, sessile, bracteate at the base, the bracts numerous and closely imbricate, cupuliform, brown, smooth. Sepals 5, white on the inner side, rufous-velutinous on the outer side, oblong, united at the base, acuminate, about 3.5 cm. long and 1.5 cm. broad. Petals little longer than the calyx, white, oblong-obtuse, about 3.5 cm. long and 1.4 cm. broad. Stamens inferior, numerous, in several rows, coalescent at the base, with white filaments and yellow anthers, about 3 mm. long. Ovary globose, green, glabrous, with a heavy style and a very large, conico-globose, 5-lobed, yellow stigma (according to Dewevre). Fruit globose, 2.5 cm. broad, with three parietal placentas" (De Wildeman and Durand, 1899).

Judging from the descriptions, this species is a near relative of *B. nigritana*. De Wildeman and Durand compare it with that species, and in a later publication De Wildeman (1908, p. 248) writes that *B. Dewevrei* is "perhaps only a variety" of *B. nigritana*. Gilg (1908, *loc. cit.*), however, says: "this species is very closely allied to *B. fistulosa* Mast., yet, I presume, distinct from it. The broad, thick, leathery leaves are different, as also the larger flowers, and above all is the fact that the flowers are inserted as a rule 3 or 4, rarely 5, together in the axils of the leaves."

Only known thus far from the Belgian Congo: Lower Congo: Sabuka (Em. and M. Laurent); Leopoldville (March 26 and May 19, 1915; J. Bequaert; Coll. Nos. 7173 and 7663). Kasai: Dina; cliffs of Batempa; along the Sankuru; Kondue; Bena Dibehe; Olombo (Em. and M. Laurent); Bena Makima; Bombaie (Leserauwact). Middle and Upper Congo: Bolombo; Inongo (Em. and M. Laurent); Bangala, type locality (Dewevre; Hens). Eastern Congo Forest; Yalutcha; Yanonge (H. Kohl).

Barteria fistulosa Masters

Barteria fistulosa MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' V, p. 511. K. SCHUMANN, 1890, Verh. Bot. Ver. Brandenburg, XXXI, 2, p. 121, footnote. A. ENGLER, 1892, Engler's Bot. Jahrb., XIV, p. 392. WARBURG, 1894, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' III, pt. 6a, p. 27, fig. 2B. E. DE WILDEMAN AND TH. DURAND, 1901, 'Reliquiae Dewevreanae,' p. 98 (type and variety *macrophylla*). H. WINKLER, 1906, Engler's Bot. Jahrb., XXXVIII, pp. 259-260. E. DE WILDEMAN, 1906, 'Mission Emile Laurent,' fasc. 3, pp. 250-258, Pls. XCI and XCII; 1907, 'Études Flore Bas- et Moyen-Congo,' II, 1, p. 57; 1908, *ibid.*, II, 3, p. 316. H. WINKLER, 1908, Aus der Natur, III, p. 661. GILG, 1908, Engler's Bot. Jahrb., XL, p. 480. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 97-108. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 223. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, 2, p. 642, fig. 553B. J. GILLET AND E. PAQUE, 1910, 'Plantes Principales Kisantu,' p. 81. GILG, 1913, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 568. E. DE WILDEMAN, 1920, 'Mission de Brier au Mayumbe,' pp. 104, 203, and 255.

"A small tree with angular, smooth or lenticellate, fistular branches. Leaves leathery, 10 to 12 in. long, 3 to 4 in. wide, oblong, obtuse, glabrous, 1-nerved, somewhat narrower at the base which is decurrent along the branch. Stipules 0. Flowers sessile, in linear clusters emerging from the stem between it and the decurrent edges of the leaf, each encircled at the base by numerous overlapping leathery shiny chestnut-colored oblong obtuse or boat-shaped bracts, increasing in size from below upwards. Flowers smaller than those of *B. nigritana*. Sepals and petals downy on the outside, lanceolate, wavy at the margins. Corona and inner organs of the flower as in the last-named species, but smaller. Anthers apiculate.

"The so-called decurrent leaves would probably be more correctly described as congenitally adnate to the branch for some distance. The manner in which the flowers emerge from between the sides of the base of the leaf and the stem is very curious" (Masters, 1871).

De Wildeman and Durand's variety *macrophylla* (1901) was based on specimens with larger leaves (25 to 35 cm. long; 14 to 15 cm. broad); but, as De Wildeman observed later, this variety cannot stand, because the shape and size of the leaves in this species are extremely variable: "the normal obovate-elliptic shape, rather broadly cuneate at the base, may change in terminal leaves into elongate obovate-lanceolate, very long-cuneate at the base and reaching a length of 27 cm. by a width of 7 cm. In other forms. . . broadly obovate, shortly attenuate leaves reach a length of 38 cm. and a width of 16 cm." ('Mission Emile Laurent,' p. 249.)

According to H. Winkler (*op. cit.*, p. 260, footnote) there are two forms of *B. fistulosa* in Cameroon: "In one of them the lateral hollow branches inhabited by the ants are longer, the leaves are larger and inserted on the branch by a broader base. In this form the fruits are mostly divided into four, while in the other form they often consist of 5, or even 6, carpels. There was also a clear and characteristic difference in the shape of the seeds; while in the first variety they are 6 to 7 mm. long, 3.5 to 4 mm. wide and 2 mm. thick, the seeds of the other which were the same length measured only 3 mm. in width or even less, being thus much more slender."

Fernando Po, type locality (Mann).

Cameroon: Victoria (Wederbauer; Winkler); Barombi (Preuss; Staudt); Bpindi (Zenker).

Belgian Congo: Lower Congo: Tumba (Em. and M. Laurent); Kisantu (Gillet); Thysville (June 4, 1915; J. Bequaert). Kwango: Madibi (Lesrauwaet). Kasai: Dima; Manghe; Loukala; Olombo (Em. and M. Laurent); Bachi-Shombe (Lesrauwaet). Middle and Upper Congo: Ibali; Inongo; Eala; Botuma; Bolombo (Em. and M. Laurent); Coquilhatville (Dewevre); Lake Leopold II (Body); Betutu (Bruneel); Barumbu (October 28 and November 17, 1913; J. Bequaert; Coll. Nos. 1003 and 1209). Eastern Congo forest: Stanleyville (Dewevre; February 1915; J. Bequaert and H. Lang); Romee; Yangandi; Yalutcha; Yanonge (H. Kohl); Avakubi (January 17, 1914; J. Bequaert); Penge and at many places in the forest between Penge and Irumu (February 1914; J. Bequaert; Coll. No. 2339); Moera near Beni; between Mawambi and Avakubi (Mildbraed); in the forest between Walikale and Lubutu (January 1915; J. Bequaert). Mr. H. Lang also photographed at Medje what is evidently this species. Mayombe: Ganda Sundi (de Briey).

Winkler (1906, pp. 259-260) has published some interesting morphological and ethological notes on *Barteria fistulosa* studied by him at the Botanical Garden of Victoria, Cameroon.

One of the flowering periods, —if there be more than one—starts in March. The large white flowers are crowded together side by side on the broad base of the leaves. They seem to open with dawn and the anthesis apparently lasts a few hours only. I have not found nectar in them and never observed pollinating insects; bugs and little beetles which are often found in the flowers, have, I presume, hardly to be considered as such; nor, as it seems to me, the ants which inhabit the tree. The fruits ripen about 3 months after the flowering. They have the shape of a walnut, and are 3.5 to 4 cm. long with a diameter of 27 to 30 mm. They are flattened on two sides at the base by pressure against one another. They have four distinct protuberances at the apex, the stump of the style being placed between the four grooves. The fruits which I picked were covered at their base by the brown, closely appressed calyx;¹ however, the latter apparently remains on the tree when the ripe fruit drops. The consistency of the fruits can best be compared with that of a celluloid ball. The numerous, parietal placentas are arranged on four longitudinal bands. Each seed is enveloped by an arillus-like pulp, which has an agreeable, sweet-sour flavor; the pulp of the various seeds fills the fruit with a slimy mass. The seed is flattened, of rounded-rhomboid shape, with a small umbilicus and a network of dimples on the surface. To be sure the seeds are scattered by animals, which trace the pulp. The genets which I kept in captivity preferred these to almost all fruits. I have found, on fruits still adhering to the tree, holes the size of a hazelnut or an entire half of the pericarp lacking; the seeds together with the arillus had disappeared. Traces of bites could be distinctly recognized on a number of fruit envelopes which I found at some distance from one of the trees; they certainly were not from a bird's bill, but from teeth, probably of fruit-eating bats.² When compressed, and consequently also when bitten, the fruits split open at the top in the form of a cross between the grooves; but they open by themselves only when rather intensively drying.

¹The author evidently means the involucre of bracts, not the true calyx.

²In the African Rain Forest fruit bats undoubtedly are important agents in scattering the seeds of many fruit-bearing trees. See the remarks on this subject by H. Winkler (1906, p. 236) and H. Lang and J. P. Chapin (1917, Bull. Amer. Mus. Nat. Hist., XXXVII, p. 484).

Barteria nigritana J. D. Hooker

Barteria nigritana J. D. HOOKER, 1860, Journ. Linn. Soc. London, Botany, V, p. 15, Pl. II, figs. 1-5.

Barteria nigritana MASTERS, 1871, in Oliver, 'Flora of Tropical Africa,' II, p. 510. H. WINKLER, 1906, Engler's Bot. Jahrb., XXXVIII, p. 260, footnote. GILG, 1908, Engler's Bot. Jahrb., XI, 1908, p. 479; 1913, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-08),' II, p. 568.

Barteria Braunii ENGLER, 1892, Engler's Bot. Jahrb., XIV, p. 392. WARBURG, 1894, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' III, pt. 6a, p. 27, fig. 2A. ENGLER, 1910, 'Die Pflanzenwelt Afrikas,' I, 2, p. 642, fig. 553A.

"A small tree or shrub with stout branches, covered with rusty down, and marked on either side with a raised line continuous with the base of the leaves. Leaves coriaceous glabrous, 6 to 10 in. long, 2 to 3 in. wide, oblong, subacute, erenulate or entire; unicostate, rounded at the base or tapering into a short, thick leaf-stalk. Stipules deciduous. Flowers large, 1 to 1½ in. in diameter, sessile or subsessile in axillary tufts, each tuft consisting of 2 to 4 flowers, each of which is invested in a series of overlapping coriaceous chestnut-colored acute or cuspidate bracts. Flower-tube very short, glabrous. Sepals 5, somewhat coriaceous, oblong-lanceolate or obtuse, downy and golden brown on the outer side, smooth and whitish within. Petals oblong, wider than the sepals and about equal to them in length, white. Stamens hypogynous or slightly perigynous; filaments slender. Ovary smooth; style simple, as long as the filaments and terminated by a large conical or cushion-shaped stigma. Fruit ovoid, about the size of a pigeon's egg, coriaceous, reddish, 1-celled, with numerous compressed pitted seeds attached to parietal placentas" (Masters, 1871).¹

Southern Nigeria: Nun River, type locality (Barter); Bonny River (Mann); Old Calabar (Thomson).

Cameroon: Batanga (Dinklage); Kribi (Zenker).

Spanish Guinea: on the coast of Bata near Campo (Busse).

French Congo: on the Gaboon River near Libreville (Mildbraed).

As pointed out by Gilg this species seems to be restricted to the coastal forest belt ("eine echte Seestrandspflanze") which grows inland of the mangrove formation along the Gulf of Guinea. Similar patches of dense forest are to be found immediately landward to the mangroves in the estuary of the Congo, but I have never seen any *Barteria* there.

Barteria nigritana variety *uniflora* De Wildeman and Durand

Barteria nigritana variety *uniflora* E. DE WILDEMAN AND TH. DURAND, 1900, 'Contributions Flore du Congo,' II, p. 24; 1900, Bull. Herbar Boissier, (2) I, p. 22. E. DE WILDEMAN, 1904, 'Etudes Flore Bas- et Moyen-Congo,' I, p. 169. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 109. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 224.

¹J. D. Hooker's original diagnosis is as follows: "Frutex robustus, habitu *Smeathmannia*, foliis 6-10" long., 2-3" lat., nervis primariis numerosis. Stipulae deciduae, non vlam. Flores sessiles, circiter 1-1½" diametro, in *Smeathmannia* subiniles. Bractea numerosa arcte imbricata, alabastrum maturum velantes, late ovatae cuspidato-acuminatae. Petala calyce paulo longiora. Stamina perplurima. Ovarium glaberrimum. Fructus magnit. ovi columbae."

"A high tree, with thick branches, which are striate, ferruginous-pubescent, marked on either side with a raised line connecting the leaf-bases. Leaves alternate, shortly petiolate; the petiole 5 to 6 mm. long and 3 mm. broad; oblong, subacuminate, 11 to 17 cm. long and 3.7 to 5.5 cm. wide, entire, shiny above and below, dark above, paler below, the upper side subglabrous or with a few scattered hairs; the under side with short, sparse, brown pilosity, especially on the veins; lateral nerves a little prominent above and below, arcuately anastomosing towards the margin and prominent in the more or less recurved margin. Flowers sessile, solitary in the axils of the leaves; at the base with closely imbricate bracts, which are scarious, brown, pilose externally, embracing. Calyx with ovate-lanceolate lobes, ferruginous pilose on the outer side, glabrescent on the inner side, acuminate, 3 cm. long and 12 mm. wide. Petals equal to the sepals but completely glabrous. Corona erect, membranaceous, fimbriate-lacerate at the apex. Stamens numerous, with connate filaments. Ovary globose, with parietal placentas, and numerous ovules; style solid; stigma very large, 6 to 7 mm. broad, conico-globose" (De Wildeman and Durand).

Belgian Congo: Lower Congo: Forest of Talavanje, type locality (Cabra); Kisantu (J. Gillet).

It seems doubtful whether this form is really a variety of *B. nigritana* in view of its occurrence inland far from the coastal belt. It may possibly be specifically distinct or constitute a form of *B. Deweyrei*, a species commonly found in the Lower Congo. From the description, it appears very similar to *B. Stuhlmannii*.

Barteria Stuhlmannii Engler and Gilg

Barteria Stuhlmannii ENGLER AND GILG, 1908, Engler's Bot. Jahrb., XL, p. 479.

Barteria nigritana WARBURG, 1895, in Engler, 'Pflanzenwelt Ost-Afrikas,' C, p. 278 (not *nigritana* Hooker).

"Shrub or tree with fistulose branches, which are densely and very shortly fulvo-pilose when young. Leaves ovate or ovate-oblong, very seldom oblong; acute or often shortly and broadly acute-acuminate at the apex, rounded toward the base, though narrowed at the very base into a 6 to 8 mm. long petiole, on both sides of which there is a 3 to 4 mm. wide wing; leaves obsoletely sinuate-denticulate, or more often sub-entire, with cartilaginous margin, glabrous above (except on the median nerve), very sparsely and shortly pilose below, leathery, with 13 to 15 pairs of lateral nerves which run almost straight to near the margin where they unite by curves; with numerous transverse nerves running parallel to each other and strongly prominent on both sides; other reticulate veins almost absent. Flowers solitary or occasionally by twos in the axils of the leaves. Bracts enclosing the flower in an involucre, coriaceous, with scattered fulvous pilosity on the back. Outer sepals entirely covered on their outer side with dense fulvous pile, which on the back of the inner sepals forms only a median vertical line; otherwise glabrous, oblong, with very acute apex. Petals a little shorter than the sepals, but similar in shape, very tender; glabrous. Outer corona membranous, glabrous, about half the length of the petals, unevenly incised and fimbriate; inner corona much shorter, thickened, forming a raised ring which is distinctly but feebly emarginate and furrowed. Stamens numerous, coalescent at the base into a tube. Ovary short, turbinate, glabrous, with 4 parietal placentas. Style elongate, reaching the anthers, thick, gradually thinner upwards, ending in a very

thick, head-shaped stigma. Fruit subglobose; the pericarp parchment-like or chartaceous, fragile; seeds numerous, inserted on 4 parietal placentas, oblong, yellowish, with pitted testa.

"The winged petiole is 6 to 8 mm. long and, with both wings spread, 7 to 9 mm. wide. The swollen, hollow stalk is 6 to 10 mm. thick. The blade of the leaf is 16 to 19 cm. long, 7 to 9 cm. broad. The bracts which enclose the base of the flowers are 7 to 9 mm. long and equally wide. The outer sepals are about 2.5 cm. long, 1 cm. wide;

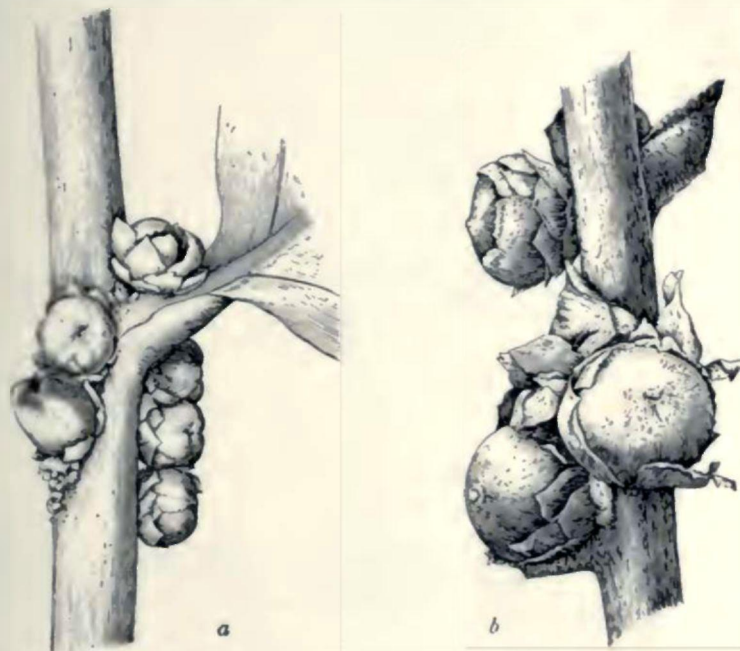


Fig. 85. a, *Barteria fistulosa* Masters: portion of branch with fruits along decurrent leaf base; b, *Barteria Deweyrei* De Wildeman and Durand: portion of branch with fruits clustered in axils of leaves (after De Wildeman, slightly modified).

the inner ones decrease gradually. The petals are about 2.2 cm. long, 8 to 9 mm. broad. The style is about 1.5 cm. long, the stigma 4 mm. long and 3 mm. thick at the base. The fruit has a diameter of about 2.5 cm. The seeds are 5 mm. long, 3 mm. wide and 1.5 mm. thick" (Engler and Gilg, 1908).

German East Africa: Bukoba, type locality (Stuhlmann).

This plant will, I believe, prove to be identical with *B. acuminata* E. G. Baker (see above, p. 425), described from Musozi on Lake Victoria, which is practically the same locality as Bukoba.

During my travels in the Belgian Congo, I came across two species of *Barteria*, *B. Deweyrei* and *B. fistulosa*. The latter is by far the more common and can be best recognized by the very peculiar way in which it

grows, by the basal swellings on some of its horizontal branches, and especially by its inflorescence. In this species a number of flowers or fruits are placed close together in a row on either side of the petiole from the axil along the decurrent base of the leaf (Fig. 85a). In *Barteria Deucevri*, however, the flowers or fruits occur either singly in the axils of the leaves or two to four together in loose axillary clusters (Fig. 85b). The anatomical structure of the two species also shows certain differences, which have been pointed out by Prof. Bailey (Part V, p. 599).

ECOLOGY OF *Barteria fistulosa*

Perhaps the most striking of Congo myrmecophytes, this plant occurs throughout the entire Rain Forest belt, where it favors the higher, more open spots, being rarely met with in damp soil. In the Savannah of the Lower Congo and Kasai District it follows the forested banks of water courses. The natives of the forest are familiar with the plant and aware of its being inhabited by very aggressive ants. When clearing the underbrush to establish a road or plantations, they usually avoid the unpleasant task of cutting this small tree. Thus it happens that *Barteria* is frequently found standing by itself in the center or near the sides of forest paths (Pl. XXIX). For the same reason, it is often met with in secondary forest growth. Among the Wangata, at Barumbu and elsewhere, its vernacular name is "Bakokombo," and other Bantu tribes use similar sounding designations (Monkukono, Makonkomo, Okakumbu, etc.)¹

This species is a typical element of the undergrowth of the forest. Under favorable conditions it may become a small tree, reaching a height of from 6 to 10 meters, or in exceptional cases 20 meters or more, but it is frequently much lower, 3 to 4 meters being a common average; its trunk is, as a rule, 10 cm. in diameter, though there are occasional records of over 40 cm. The trunk is simple or very little ramified, and bears long lateral branches, usually also unramified and spreading almost horizontally in all directions. The broad, alternate leaves are placed to the right and left of the branch, more or less horizontally or slightly curved upward. Due to this arrangement, the plant has a very peculiar appearance, well illustrated in the photographs taken by Mr. H. Lang (Pl. XXVIII, Fig. 1 and Pl. XXIX). Another unusual feature is the fact that most of the branches are deciduous. On reaching a certain length

¹According to J. Gillet, the natives at Kisantu, in the Lower Congo, call *Barteria fistulosa* either "Sakala" or "Nsakala," and de Brier gives "Zinzi" as its vernacular name in the region of Ganda Sundi.

they stop growing, lose their foliage, and gradually dry up; finally, these dead members are dropped by a histological process similar to that causing the leaves to fall. One always finds, therefore, a number of dead branches scattered over the ground at the base of this *Barteria*. Whether there is a law of periodicity or other rule governing this peculiarity cannot be decided at present, but so much is sure: the few flowering branches remain on the stem until after the fruits are ripe.

The lateral branches of *Barteria fistulosa* are of two kinds. The sterile branches—and, as noted, these are in the great majority—present at a short distance from their base an abrupt and conspicuous swelling which continues almost uniformly to near the apex with only slight constrictions at the nodes (Plate XXVIII, Fig. 2; Text Fig. 86). Except in

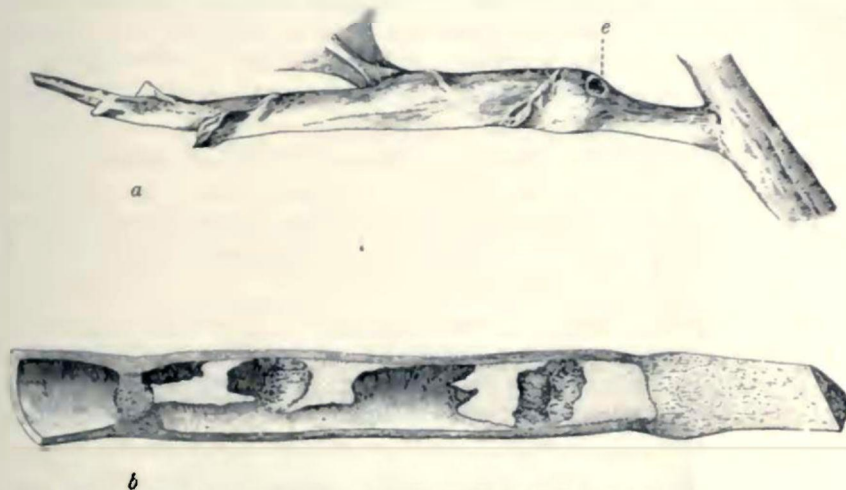


Fig. 86. *Barteria fistulosa* Masters: a, lateral branch suddenly swollen beyond its base, where it shows the circular opening (e) gnawed by the ants and leading into the domatium; about one-half natural size (after De Wildeman); b, part of longitudinal section of very young swollen lateral branch, showing gradual drying up of pith before ants gain access to the cavity; drawn from life at Barumbu, October 1913; natural size.

very young plants, these swellings are nearly always hollow and inhabited by ants. The flowering branches appear only at certain seasons, and on older trees; they are normal, not swollen, yet frequently hollowed out and also occupied by ants.

From an examination of very young specimens and others not inhabited by ants, I found that the trunk and normal, flowering branches are filled with pith and remain so unless excavated by the ants. The swollen branches (Fig. 86), on the contrary, become hollow naturally.

When young, their various internodes are at first only slightly swollen and entirely filled with soft, greenish, parenchyma; soon, however, the enlargement becomes more pronounced; the pith turns pale brownish, gradually dries and what remains finally forms brownish membranes on the inner walls or irregular partitions in a spacious cavity (Fig. 86b). The ant-chamber is thus ready for occupancy before the insects touch the branch. On uninhabited plants the sterile branches show no orifice, nor any depression or scar on their outer surface that might mark the spot where the entrance to the cavity will later be pierced by the ants. Moreover, the walls of the limb are soft and easily pressed down with the fingers, so that they must offer but little resistance to the powerful mandibles of the *Pachysimæ*.

The larger specimens of *Barteria fistulosa* that one commonly meets in the forest are, as a rule, settled by a populous colony of the large, black *Pachysima æthiops* (Emery),¹ the true body-guard of the tree. As soon as any portion of their host plant is disturbed, they rush out in numbers and hastily explore the trunk, branches, and leaves. Some of the workers usually also run over the ground about the base of the tree and attack any nearby intruder, be it animal or man. All observers agree that the sting of the *Pachysima* is exceedingly painful and is felt for several hours. Its effects can best be compared with those produced by female velvet ants (Mutillidæ; see Kohl's remarks reproduced in Prof. Wheeler's Report, p. 115). Consequently these ants are greatly dreaded by the natives and there remains little doubt that they afford a most effective protection to their host plant.

Trees inhabited by *Pachysima* are generally healthy and free from the attacks of most phytophagous insects. On specimens untenanted by ants, however, the leaves are often badly eaten by caterpillars, as I observed in two instances at Barumbu in October, 1913. On both of these trees there were also several nests of the weaver-ants, *Ecophylla longinoda* (Latreille), and numerous workers of a small *Crematogaster* running over the branches and leaves. At Penge, in February, 1914, another uninhabited *B. fistulosa* showed the live wood of its trunk badly bored by adult bostrychid beetles. On the other hand, the *Pachysimæ* are not always successful in keeping smaller parasites from their host. At Barumbu a tree occupied by a populous colony of *P. æthiops* showed numerous cecidomyid galls on its leaves. They were small fleshy swellings of the parenchyma, about equally protruding on both sides of the

¹Probably sometimes also by *Pachysima latifrons* (Emery).

leaf, and irregularly scattered. Inside of them was a single chamber containing one gall-midge larva and surrounded by a wall of coarser tissue in the center of a solid, juicy, parenchymatous mass.¹

An older, inhabited *Barteria fistulosa* may be regarded as the home of a single colony of *Pachysima* which has resulted either from the gradual growth of a small nest founded by one female, or from fusion of several nests started independently by a number of females. Both modes are possible, but the second is probably the more common. At Avakubi, in January, 1914, I had an opportunity to examine a very young *Barteria fistulosa* not over one meter high, with but six short, horizontal branches, all of which were swollen beyond the base in the usual way. Only a few of the distended internodes were settled by ants and each was a closed, separate cavity containing one dealated *Pachysima* queen; no workers, larvæ, or eggs were present. After the nuptial flight the *Pachysima* females had evidently entered the hollow internodes by gnawing through the wall. They had not again left the cavity, for the entrance was partly plugged up by callus growth. When disturbed, these gravid queen ants made no attempt to defend themselves, behaving in this respect very differently from workers. It is also interesting to note that some of the *Pachysima* females were dead and that in one such case another minute ant, of an unidentified species, had established its nest in the same internode with the remains of a dead *Pachysima* queen. A colony of *Pachysima æthiops* in a somewhat more advanced stage was found in a young *Barteria fistulosa*, at Barumbu in November, 1913. A queen ant, surrounded by an abundance of eggs and young larvæ, was found inside each of a series of swollen internodes, all still separated by the nodal partitions. Here, too, a growth of callus had partly closed the entrance which had been further plugged with dried particles of pith evidently brought there by the female. Since the older *Barteria* is finally occupied by one single colony, all the members of which live and work peacefully together and enter indifferently the various domatia, the initial formicaries in all probability fuse into one. The workers in such a formicary not only enlarge the exit holes, which are usually placed at the base of the swelling toward the upper face of the branch, but also clean the cavities of the remains of dried pith and pierce the partitions between the various internodes. Each lateral branch finally forms one continuous gallery.

¹Lamborn (1914, p. 493) notes that he once found larva and pupa of *Tinthia lambornella* Durant, an ægeriid moth, in an internode of a *Barteria* in Southern Nigeria; this cavity was separated from the adjoining internodes, both of which were inhabited by *Pachysima æthiops*.

The origin and growth of new colonies of *Pachysima* in *Barteria* deserves to be further investigated in the field. Perhaps such a study will show us typical examples of secondary pleometrosis, or founding of an insect society through fusion of a number of colonies each started independently by a fertile female. H. v. Ihering (1907) believes *Cecropia adenopus* is settled in this manner by *Azteca mulleri*. Furthermore, in his opinion, all but one of the fertile queens inhabiting the same tree are eventually killed by the workers, a conclusion drawn from the presence of a sole queen in each adult *Cecropia*. It will be important to look into conditions in this respect in the *Pachysima* formicaries of *Barteria*.

The *Pachysimæ* undoubtedly derive certain advantages from living inside *Barteria*. The hollow, nearly horizontal branches provide very convenient nesting chambers, where the brood is kept in safety under almost ideal conditions of aeration, temperature, and humidity. Whether the ants also procure part or all of their food from the host is still doubtful. Kohl has often seen the workers actively licking nectaries at the insertion of the leaves, and also gnawing the young bark and the epidermis on the upper and under sides of the blades; they are particularly fond of the very young flowers, which they frequently destroy almost completely. Certain other insects live in the domatia with the ants, the most common of these companions being coccids (*Pseudococcus citri* variety *congoensis* Newstead) which, I am inclined to think, are not brought in by the ants, but migrate inside the swellings of their own accord. I have found this to be also the case with scale insects living in the myrmecodomatia of *Cuviera*. Even in very young *Barteriæ*, of which only a few internodes are occupied by queen ants and their brood, one discovers coccids in the cavities. Another interesting inquiline of *Barteria* is a minute phorid fly, *Hypocera tristis* H. Schmitz, noticed by Father Kohl near Stanleyville in swellings of *Barteria fistulosa* occupied by *Pachysima æthiops* (Wasmann, 1915a, p. 320, footnote).

Whether the coccids of *Barteria* are really attended by *Pachysima* for the sake of their excretions remains uncertain. Wheeler and Bailey (1920, pp. 261-262) have dissected the pellets contained in the infra-buccal pockets of workers and the trophothylaces of larvæ of *Pachysima æthiops* and *P. latifrons*. They were much the same in both species and consisted of pieces of coccids or whole, crumpled-up bodies of young scale insects, fungus spores, bits of mycelium, portions of plant-tissue evidently gnawed from the walls of the cavities, pollen-grains, etc. In a few of the pellets Prof. Bailey found small nematodes resembling the species of *Pelodera* described by Janet as living both as parasites in

the pharyngeal glands of certain European ants and as free organisms in the detritus of the nest.

A thorough investigation of the feeding habits of both adult and larval *Pachysimæ* in *Barteria* will be the most important problem to be studied in the future. In this connection, it may be well to note a peculiarity to which my attention was directed by my friend, Mr. J. P. Chapin, during our stay at Avakubi in January, 1914. When *Barteria fistulosa* inhabited by *Pachysima* occurs in rather dense forest, one frequently notes about its base an open patch, fifteen to twenty feet in diameter, where most of the heavy undergrowth has been cleared away. Only a few, low herbaceous plants and often also the slender leaf-stalks of the common marantaceous forest reed, *Sarcophrynium Arnoldianum* De Wildeman, are left standing. The ground at the foot of the tree is partly covered with fallen leaves and dead branches of the *Barteria*. One can always find a few *Pachysima* workers running over this open space, for a purpose unknown to me, perhaps in search of insects which may form part of their diet.¹ I merely venture the supposition that the ants themselves are instrumental in preventing the growth of heavy vegetation near the base of their shelter, perhaps by nipping the tender shoots of the young plants.² One can readily imagine that such a clearing would be of use to the ants in their hunts for other insects, making the capture of their prey so much easier and quicker. Incidentally, *Barteria* too may be benefited, since it is saved competition with more vigorous species of trees or shrubs, which, if allowed to thrive near its trunk, would soon interfere with its growth. The shade given by *Barteria fistulosa* is so slight that this factor alone could not account for the absence of woody vegetation within a radius of six to eight feet from its base.³

As soon as the leaves of *Barteria fistulosa* fall, the branches begin to dry up, but remain on the tree for several weeks before being shed as described above. Then, however, they are not occupied by the *Pachysimæ*, which pay no further attention to them, one proof more of the strict, obligatory relations existing between these ants and the host plant. The empty, dried swellings may be temporarily occupied by other, small

¹My observations do not agree on this one point with those of Father Kohl, who believes that *Pachysima* never leaves *Barteria* "since they do not undertake hunting parties for strange insects."

²With regard to this interesting point I quote the following passage from Kohl's paper (1909): "Some natives assured me that the *Nimæ* (= *Pachysimæ*) occasionally trim to half its height the low vegetation which surrounds their host plant. I once observed similar, partly cut low plants in the vicinity of my Mission, but I did not guess the possible agent of this."

³Ule (1907, p. 131) also remarks that *Pseudomyrma dendroica* Forel and *P. triplarina* Forel, which live inside stems and branches of *Triplaris Schomburkiana* along the Juruá River, Brazil, run down to the ground, where in a circle a few meters wide no other vegetation is allowed to grow.

species of ants. At Barumbu, in October, 1913, I came across a *Barteria fistulosa* whose living branches were inhabited by *Pachysima xthiops*, while the dead twigs, still attached to the tree, contained small colonies of a *Crematogaster*. These little ants were apparently not molested by their large neighbors, but, when the tree was disturbed, they remained safely inside, while the *Pachysimæ* rushed forth and ran feverishly over the plant.

The myrmecophytic nature of *Barteria fistulosa* was first recognized by K. Schumann (1890, p. 121, footnote) on herbarium specimens collected in Cameroon. Some of the swellings cut open by him still contained a few *Crematogasters*. Its relations with ants were studied in the field by A. Dewevre (De Wildeman and Durand, 1901, p. 98), Emile Laurent (De Wildeman, 1906, pp. 250-258), H. Winkler (1906, p. 59), and H. Kohl (1909, pp. 97-108). Mention is made in Prof. Wheeler's Report (p. 114) of some of these earlier observations which agree in most details with my own.

The following ants have been found thus far in the swellings of *Barteria fistulosa*, but the two species of *Pachysima* alone can be regarded as obligatory guests of the plant. The others are all accidental tenants which nidify in other places also; they are usually met only on plants or in branches which for some reason or other have been left by the *Pachysimæ*.

Pachysima xthiops (F. Smith). The large, black ant which is the regular inmate of *Barteria fistulosa*, was first collected in this plant by Father Kohl, near Stanleyville (1909, p. 106), and sent by him for identification to Forel (1916, p. 403). Both Mr. Lang and I commonly found the same species at Medje, Ambelokudi, Barumbu, Avakubi, etc.¹ The scale insect *Stictococcus formicarius* Newstead was found by Kohl near Stanleyville with these ants (Newstead, 1910, p. 19).

P. latifrons (Emery). Specimens of this species obtained by Mr. H. Lang at Niangara were probably taken from *Barteria fistulosa*.

Tetraponera anthracina (Santschi). Near Stanleyville (H. Kohl; see Forel, 1916, p. 403). I found several workers of this species at Thysville (June 1915) running over the leaves and twigs of a *Barteria fistulosa* whose swellings were free of ants; I did not find their nest.

¹*Pachysima xthiops* was originally described from South Africa, without indication of collector. No species of *Pachysima* has since definitely been recorded from that part of the continent. Since the genus is restricted to *Barteria* and *Myrmecia*, which are not known to occur south of 7° S. lat., there is a question whether Smith's type was wrongly labeled. It is, however, not so clear how he could have received West African specimens of *P. xthiops* at a time (1877) when hardly any myrmecological collections had been made in Equatorial Africa. I am rather inclined to believe that Smith's type was obtained in the forests of Natal from a myrmecophyte which has since escaped notice.

T. mocquerysi (Ern. André). Near Stanleyville (H. Kohl; see Forel, 1916, p. 403).

T. oberbecki (Forel). Leopoldville (H. Kohl; see Forel, 1916, p. 403).

T. ophthalmica (Emery). Stanleyville and Bengamisa (H. Kohl; see Forel, 1916, p. 403). I collected workers of this ant at Thysville, together with *T. anthracina*, as mentioned above.

T. prelli (Forel) variety *odiosa* (Forel). Belgian Congo (H. Kohl; see Forel, 1916, p. 403).

Crematogaster excisa subspecies *impressa* (Emery). Discovered by Kohl (1909, p. 103, footnote) in branches of *Barteria fistulosa* collected by Ém. Laurent at Isangi. Also near Stanleyville (H. Kohl; see Forel, 1909b, p. 69).

C. impressiceps (Mayr). Taken from hollow twigs of *Barteria fistulosa* by Mr. H. Lang at Panga.

C. striatula Emery. Romée near Stanleyville (H. Kohl, 1909, p. 167).

ECOLOGY OF *Barteria Deucecei*

This species is less common than the preceding and has been but little studied so far. The following notes were made on specimens I found near Leopoldville, in one of the small patches of forest which are scattered through the savannah of that region (March, 1915) and also in a forest gallery along one of the small affluents of the Congo (May, 1915). In that locality, it is a low tree, rarely over 6 meters high, with a straight, simple, or feebly ramified trunk, 20 cm. thick at the base. The alternate leaves are more elongate-elliptic than in *B. fistulosa*, being as much as 40 cm. long and 9 cm. wide. The lateral branches on my specimens were all alike, feebly branching and irregularly spreading, giving the tree a very different appearance from that of the species just mentioned. The specimen collected in May was in flower.

There were no swellings on any of these plants from Leopoldville, but all the lateral branches (Fig. 87a-b) were hollowed out almost their entire length, each with one continuous cavity. Only the upper extremity of young branches was still filled with green, soft pith, which seems to dry up very soon, as the pith channel is hollow 6 cm. from the tip. A few entrances to the inner cavities had been pierced, mostly on the upper side of the branch, at intervals of about 6 to 14 cm. from one another, usually a short distance above the insertion of a leaf.¹

¹One of the specimens of *B. Deucecei* from Leopoldville answered well the description given by Em. Laurent, of a plant which he found at Dima, along the Kasai: "Branches laterales raminees, ce qui donne a l'arbre de 6 ou 7m. de haut, un tout autre aspect (que chez *B. fistulosa*); ces branches de 3 a 4 cm. de diametre sont habitees par des fourmis et leur canal medullaire de 3 mm. de diametre, resterait apres 3 ou 4 ans de vegetation toujours habite par des fourmis noires tres petites. Beaucoup de rameaux sont perfores seulement au sommet et les fourmis en habitent surtout la region terminale. Les feuilles, largement ovales, luisantes sur les deux faces, ont un petiole de 10 a 15 mm. de long, le limbe mesure de 30 a 36 cm. sur 14 a 16 cm. et porte 10 paires de nervures laterales" (De Wildeiman, 1906, p. 250). Laurent believed that this plant was a species of *Barteria*, but this was doubted by De Wildeiman.

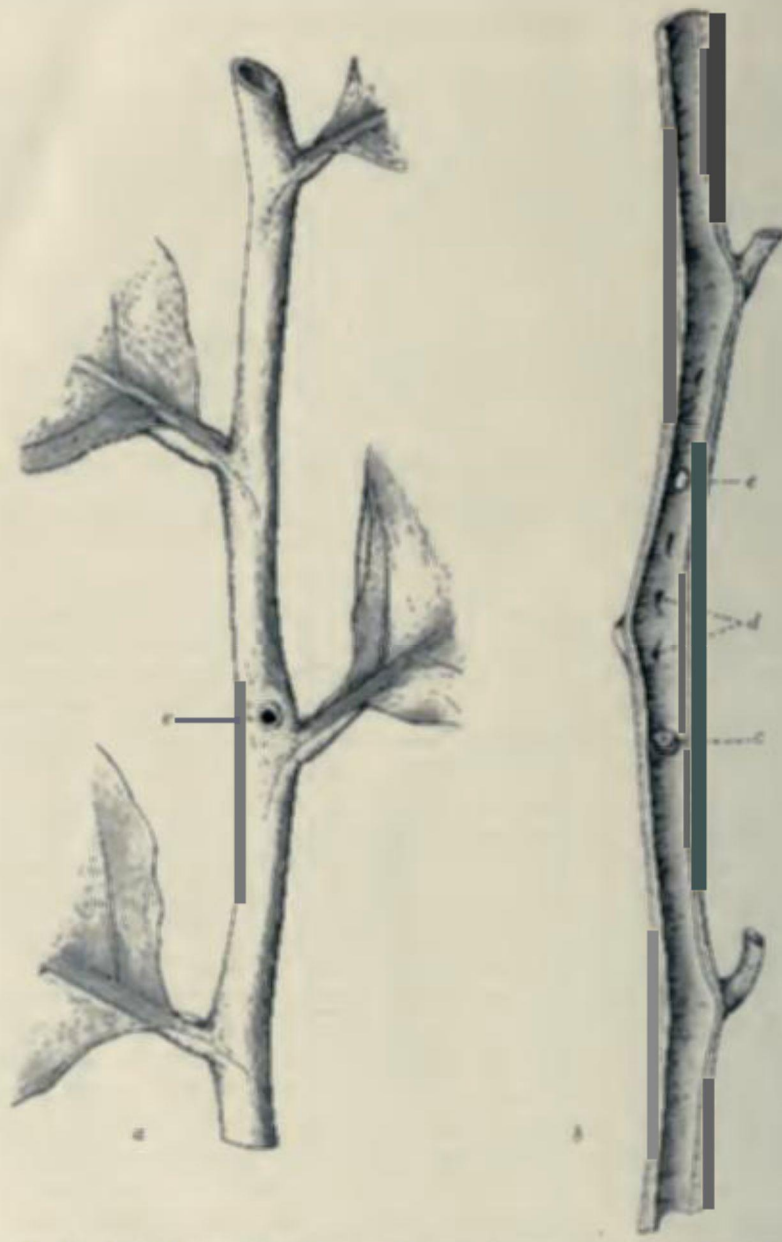


Fig. 87. *Barteria Deweyi* De Wildensan and Durand: *a*, external view of portion of lateral branch inhabited by ants; *b*, longitudinal section of this branch, showing a coccid (*c*) fixed on inner wall and small depressions (*d*) in which scale insects are often found; *e*, orifice leading into the dermatium. Drawn from life at Leopoldville, March, 1915; natural size.

The hollow branches of the two specimens of *B. Dewevrei* examined contained colonies of *Crematogaster africana* variety *schumanni* (Mayr), with a queen, workers, and brood; also some coccids which were usually in a small, scar-like depression in the wall. In one tree some of the branches contained insect larvæ, a lepidopterous pupa, and an adult beetle, but these were in cavities quite separate from those inhabited by ants.

Dewevre, who discovered this species in the Bangala region, on the Upper Congo, mentions finding ants in its hollow branches (De Wildeman and Durand, 1901, pp. 97-98). A few notes on its relations with ants were also made by Ém. Laurent (De Wildeman, 1906, pp. 247-250) and H. Kohl (1909, pp. 108-109). The following ants have been found in its myrmecodomatia:

Pachysima æthiops (F. Smith). Dima (Ém. Laurent; see H. Kohl, 1909, p. 108); Yalutcha and Yanonge (H. Kohl, 1909, p. 108).

Crematogaster africana (Mayr) variety. Dima (Ém. Laurent; see H. Kohl, 1909, p. 108).

C. africana variety *schumanni* (Mayr). Leopoldville (J. Bequaert).

Apocynaceæ

EPITABERNA K. Schumann

Epitaberna K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 316.

"A bush with branches thickened and hollow below the nodes. Leaves large, short petiolate, lanceolate, short acuminate. Flowers diclinous, showy, axillary; their pedicel with a pair of lower bracteoles, simulating interpetiolar stipules, and also with a second pair of bracts below the ovary. Sepals large, foliaceous, subinequal, alternating with very large, linear, solitary glands. Corolla very large, infundibuliform: its lobes ample, curled along the margin, their sides in the bud inflexed and covering each other dextrorsely; its throat with variegated hairs. Stamens inserted near the throat, without any stiff appendage at the base, acute and not appendiculate at the apex. Ovary perfectly inferior, pentapertous, 2-celled; with numerous ovules inserted on a thickened placenta; disc annular; style thickened and bilobed at the apex. Fruit unknown.

"Only one species is known.

"The genus is a relative of *Taberna montana*, from which it differs in its completely inferior ovary and in the large sepals" (K. Schumann, 1903).

This is the only genus of the large family Apocynaceæ which has thus far been recognized as a myrmecophyte and the true nature of its relations with the ants has apparently not been further investigated on living specimens. It contains only one species.

Epitaberna myrmæcia K. Schumann

Epitaberna myrmæcia K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 317.

"Branches thickened at the nodes, quadrangular, glabrous. Leaves short petiolate, lanceolate, ample; short and sharply acuminate, acute at the base, glabrous above; slightly hairy on the under side in youth and later on with scattered pile on the midrib. Flowers short pedunculate. Ovary glabrous. Sepals lanceolate, acuminate, large, glabrous. Corolla with a tube extending hardly beyond the calyx; glabrous outside; densely villose at the throat on the inner side; the lobes broadly elliptic, acuminate, curled along the margin, twice the length of the tube, lanceolate in the bud. Stamens linear, enclosed. Style glabrous, filiform, thickened at the apex.

"The flowering branches, 15 cm. long, are 2 mm. thick in the middle of the internodes; the upper part of the internodes is swollen into a spindle-shaped cavity with thin walls, which is as much as 5 cm. long and 9 mm. in diameter and serves as a myrmecodomatium. The heavy, glabrous petiole is grooved on the upper side and at most 5 mm. long. The blade has a length of 11 to 28 cm. and a greater width of 5.5 to 11 cm. in the middle; it is crossed on each side of the midrib by 6 to 10 stronger veins, which are prominent on both sides; in dried condition it is dark green above, pale green below. The flowers do not always present an ovary, there being male and female flowers; but otherwise they do not differ from each other. The peduncle is 5 mm. long, and the inferior ovary about the same length. The green sepals reach a length of 2.5 cm. The tube of the white corolla, with its chrome-yellow throat, is 2.2 cm., and its lobes 5.5 cm. long. The stamens are inserted at 15 mm. above the base of the corolla; the anthers are 7 mm. long. The style measures 1.3 cm.

"The plant is remarkable, representing a new case of myrmecophily. I myself have collected the ants from the wool of the throat of the corolla. This is the first case of completely epigynous flowers among the Apocynaceæ; accordingly the fruit is probably also synecarpous" (K. Schumann).

Cameroon: Bipindi (Zenker).

Epitaberna myrmæcia probably occurs throughout the forest of southern Cameroon and Spanish Guinea. According to Stitz (1910, p. 131), Tessmann found inside the caulinary swellings of this plant, the large *Pachysima æthiops* (F. Smith) (= *spininoda* André) which the Pangwe call "engunkun," much fearing its sting in the belief that it causes fever.

Tessmann, in his account of the Pangwe of southern Cameroon and Spanish Guinea, describes how the tribe uses this myrmecophyte in one of their religious ceremonies. During the initiation to the "Sso-cult" of the Yaunde, the candidates are obliged to pass for several days through a succession of tests, one of which is as follows. Nests of stinging ants, especially those of *Plagiolepis carinata* Emery, and branches of *Epitaberna myrmæcia* inhabited by *Pachysima æthiops*, are hung or placed in a low hut built for that purpose near the village. This place soon swarms with ants; pods of *Mucuna pruriens* covered with dangerously itching hairs are also thrown inside. The neophytes are then brought there and,

after being much frightened by howling and threats, are forced to crawl in succession through the ant-hut where they are, of course, fearfully stung.¹

Verbenaceae

CLERODENDRON Linnæus

Clerodendron LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 637. BRIQUET, 1895, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 3a, p. 174. J. G. BAKER, 1900, in Thistelton-Dyer, 'Flora of Tropical Africa,' V, 2, p. 292.

"Trees or shrubs, sometimes scandent. Leaves opposite, rarely ternately verticillate, entire or toothed. Cymes axillary or terminal, lax or dense. Flowers small or large, various in color. Calyx not accrescent; tube campanulate; lobes 5, equal, longer or shorter than the tube. Corolla-tube cylindrical; lobes 5, obovate, spreading or slightly reflexed, subequal or unequal. Stamens 4, inserted below the throat of the corolla-tube; filaments long, filiform, involute in bud; anthers ovoid or oblong, with parallel cells. Ovary imperfectly 4-celled; cells 1-ovuled; style long, bifid at the apex. Fruit a globose drupe with a fleshy pericarp and 4 smooth or rugose pyrenes. Seed oblong, exalbuminous" (J. G. Baker, 1900).

This is a very large genus, numbering some 200 species and distributed between the tropics in the Old World; over 150 have been described from Africa, 35 of which have been recorded from the Belgian Congo. They are very common at the edges of the forest and along rivers, where the creeping species often are one of the striking elements in the landscape, on account of their beautiful, showy flowers. The species of the savannah are most frequently low shrubs or erect or trailing herbs.

A number of species of *Clerodendron* have been found associated with ants, but the few published observations are too fragmentary to show whether any of the forms are true myrmecophytes. Among the African representatives, *Clerodendron excavatum* E. De Wildeman² is myrmecophilous according to certain observers, while others assert that its hollow stems are merely filled with water. At all events, ants were never found inside the stems of that plant.

At Penge, in January, 1914 (Coll. No. 2205), I collected on the bank of the Ituri River in the dense undergrowth of the forest a low bushy *Clerodendron* which may possibly be *C. excavatum* E. De Wildeman. The plant was 3 to 4 m. high and divested of leaves at that season of the year. Some of the branches, however, were covered with numerous, white, showy flowers, obliquely directed downward. No swellings nor domatia could be found, but the internodes of stem and branches were normally

¹Trenmann, G., 1913, 'Die Pangwe,' II, pp. 46-47.

²Described, 1900, in 'Etudes Flore Bas- et Moyen-Congo,' III, 1, pp. 132-134, Pl. XI; 1912, *ibid.*, III, 3, p. 468.

hollow, due to the early resorption and drying up of the pith. Many of the hollow internodes contained nests, with a fertile queen, workers, brood, and newly hatched winged sexual forms of a small, unidentified ant. The insects entered and left by a circular entrance pierced through the wall about half-way between two nodes. In certain cases the partition at the nodes had not been removed, whereas in others the entire limb formed one continuous nesting cavity. An internode of one of the living branches was occupied by a nest of a small solitary bee belonging to the genus *Allodape*.

In a recent note De Wildeman (1920) directs attention to several African *Clerodendrons* with fistulose stems, such as *C. excavatum* De Wildeman, *C. angolense* Guerke, and *C. carum* De Wildeman. The last named was described from specimens which I collected in the Savannah country of the northeastern Belgian Congo, near Boga (July 12, 1914; Coll. No. 5002), between Beni and Kasindi (August 9, 1914; Coll. No. 5205), and near Rutshuru (September 4, 1914; Coll. No. 5534). It is a low bush of the open grass-land, with white flowers; I never observed ants living in or on it.

Following the description of his *Clerodendron formicarum*, Guerke mentions that he saw a specimen obtained by Stuhlmann near Bukoba. Ants of the genus *Crematogaster* were living in its hollow stem, the walls being pierced by a circular hole. Guerke, however, was doubtful as to the specific identity of this Uganda specimen and the typical *C. formicarum* from Angola and the Kasai. The latter is a low, semi-herbaceous plant, 25 to 30 cm. high, which, as I have shown elsewhere, is not the myrmecophyte its name would imply. Stuhlmann's specimen from Bukoba was a rather high, much-branched shrub, with smaller flowers and there is a possibility that it belonged to *C. carum* De Wildeman, collected by me in several near-by localities.

VITEX Linnæus

Vitex (Tournefort) LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 638. J. BRIQUET, 1895, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 3a, p. 170. J. G. BAKER, 1900, in Thielton-Dyer, 'Flora of Tropical Africa,' V, p. 315.

"Trees or shrubs, with glabrous or hairy branches. Leaves opposite, usually compound, digitate, rarely simple. Cymes dichotomous, axillary or forming a terminal panicle. Flowers whitish, yellowish, lilac, or blue. Calyx campanulate or funnel-shaped, 5-toothed or nearly truncate, accrescent. Corolla-tube short or long, sub-cylindric or funnel-shaped, straight or slightly curved; limb obliquely patent, sub-bilabiate. Stamens 4, didynamous, inserted in the corolla-tube and usually exserted from it; anther-cells nearly parallel or divergent. Ovary at first imperfectly

2-celled, usually finally 4-celled; ovules solitary, laterally attached; style filiform, bifid at the apex. Drupe with a more or less fleshy mesocarp and a hard, 4-celled endocarp. Seeds obovate or oblong, exalbuminous" (J. G. Baker, 1900).

This diagnosis should be amended to include creepers also. Apart from the myrmecophilous species of the Ituri Forest described below, the creeper form was apparently thus far unknown in the genus. J. Briquet,¹ it is true, incidentally mentions *Vitex pycnophylla* K. Schumann as a creeper, but, so far, I have failed to find a species of that name described.²

The genus *Vitex* contains over one hundred species in the tropical and subtropical parts of both hemispheres. A large number of these are found in Tropical Africa, some twenty being recorded from the Belgian Congo. It is rather closely allied to *Clerodendron*, from which it can only be separated with certainty by the structure of the fruit. While in *Vitex* the endocarp of the drupe forms a single 4-celled nutlet, in *Clerodendron* each fruit contains two 2-celled or four 1-celled nutlets. In addition, all known forms of *Clerodendron* have simple leaves, either entire, toothed, or more or less lobed, whereas in *Vitex* compound, digitate leaves are the rule and simple ones the exception.

Two of the African species are definitely known to be myrmecophilous, but probably other tropical members of the genus also have associations with ants.

Vitex Staudtii Guerke

Vitex Staudtii GUERKE, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 299.

"Tree or shrub³ with quadrangular branches. Leaves 5-foliolate, with very long petioles; the leaflets petiolulate, obovate, attenuate at the base, with entire margin, ending in a very long apex, rough above, glandular below. Inflorescences terminal, thyrsoidal, loose; peduncles puberulent. Calyx cupuliform, with truncate or obsolete 5-toothed margin.

"The branches are sharply quadrangular, entirely glabrous, hollow. The opposite leaves are 5-foliolate, with a petiole 10 to 18 cm. long. The leaflets have a petiole of 5 to 20 mm.; that of the median leaflet longer than the others; they are obovate, twice as long as broad on the average, without the apex 10 to 14 cm. long and 5 to 7 cm. wide; narrowed at the base into the petiole; with entire margins; prolonged into a tip which is suddenly constricted at the base and 1 to 3 cm. long; the upper side with very short, scattered, coarse hairs; under side glabrous, but densely covered with minute, golden yellow glands. The thyrsoid inflorescences are terminal, as much as 30 cm. long, very loose with far spreading branches, which are quadrangular like the petioles, and glabrous or with feeble downy hairs toward the

¹In Engler and Prantl, 1897, 'Die Naturl. Pflanzenfam.,' IV, pt. 3a, p. 133.

²The name is not recorded in the Index Kewensis nor in any of its Supplements.

³"Arbor vel frutex." This should be amended to "creeper." See remarks at end of description.

apex; the subdivisions of the inflorescence are pseudo-umbels of 6 to 20 flowers. The peduncles are 2 to 4 mm. long, covered with fine downy hair and bear about the middle of their length 2 lanceolate, easily dropped, downy bracts, 2 to 4 mm. long. The calyx is broadly cupuliform, 3 mm. long, with a truncate or very indistinctly 5-toothed margin. The corolla is greenish-white, covered with yellow glands outside, with curved tube.

"The species belongs in the section *Agnus Castus* and more definitely in Briquet's *Terminales*-group. Among related forms, *V. Buchanani* Baker differs in the smaller, hairy leaves; *V. quadrangula* Guerke also is more strongly pilose. *V. thyrsoflora* Baker too belongs in this group, but is known to me only by the description according to which the leaves are pubescent on the under side also and the calyx apparently is more distinctly toothed. The present species is furthermore characterized by being inhabited by red ants; the hollow branches usually show at the nodes the almost circular orifices which are characteristic of so many ant-plants" (Guerke, 1903).

Togo: not rare in the forest (Baumann).

Cameroon: Yaunde (Zenker and Staudt).

Belgian Congo: Northeastern Congo Forest: Avakubi (January 1914; Lang, Chapin, and J. Bequaert; Coll. No. 1803); Medje (July 1914; Lang and Chapin); Penge (January 31, 1914; J. Bequaert; Coll. No. 2216); between Penge and Irumu (village of Nduye, February 20, 1914; J. Bequaert); Kilo (June 30, 1914; J. Bequaert; Coll. No. 4894).¹

V. Staudtii must also occur in Spanish Guinea, since its peculiar host, *Viticicola tessmanni* (Stitz), was originally found at Alen, Spanish Guinea, by Tessmann.

With the exception of the indication "tree or shrub," Guerke's diagnosis of *V. Staudtii* agrees perfectly with a myrmecophilous creeper obtained by me in the Ituri Forest and of which dried branches were also brought back by Messrs. Lang and Chapin. In the hope of identifying this plant, I have carefully read the numerous published descriptions of African *Vitex* and there is a reasonable certainty that the Ituri creeper is either identical with or very closely allied to *Vitex Staudtii*.¹ The designation "tree or shrub" is, I believe, due to the fact that Guerke based his description on a few herbarium specimens, which gave not the slightest indication that the species was a creeper; moreover, all other members of the genus known thus far are either trees or erect shrubs.

Vitex yaundensis Guerke

Vitex yaundensis GUERKE, 1903, Engler's Bot. Jahrb., XXXIII, 2, p. 296.

"Tree, with very long petiolate, 5-foliolate leaves. Leaflets short petiolulate, oblong-ovate, cuneate at the base, with entire margin, very glabrous on both sides. Flower-cymes axillary, with very long peduncles. Bracts linear. Calyx turbinate, 5-toothed, with deltoid teeth. Tube of the corolla hardly raised above the calyx.

¹Mr. Chapin informs me that he saw this myrmecophilous creeper also near Ngayu.

²The first indications as to the taxonomic position of this curious myrmecophyte were given by Prof. I. W. Bailey, who, from histological examination of the stems, concluded that it belonged to the Verbenaceae, most probably in the genus *Vitex*.

"A tree 6 to 8 m. high, with quadrangular, glabrous branches. The leaves are 5-foliolate, borne on a petiole 15 to 22 cm. long, which is glabrous with a flattened groove above. Leaflets with a petiole 1 to 2 cm. long; elongate-ovate, narrowed at the base into the petiole; with entire margin; long acuminate, herbaceous, entirely glabrous on both sides. Parallel lateral veins very numerous, as many as 25 on the median leaflet. The median leaflet reaches a length of 24 cm. and a width of 9 cm.; the two lateral leaflets nearest it are a little smaller, reaching a length of about 20 cm.; the two external leaflets are only 14 cm. long and 7 cm. wide, being in proportion broader than the two lateral leaflets. The inflorescences are placed in the axils of the upper leaves and borne on peduncles 16 to 20 cm. long; they are loose, compound double cymes (dichasia) with strikingly long ramifications. The bracts are sessile, linear, long acuminate, with fine downy hair, as much as 15 mm. long on the lower ramifications; shorter on the upper ramifications. The peduncles are 2 to 3 mm. long and covered with fine downy hair. The calyx when expanded is top-shaped, downy, 3 mm. long, 5-toothed; the teeth are triangular with even sides, rather acute, 1 mm. long and about as wide at the base. The corolla has a very thick, glabrous tube, which is only 4 mm. long; the limb is distinctly bilabiate and 5-lobed; the two posterior lobes are ovate, obtuse, downy, 1 mm. long; the two lateral ones have a similar shape and pilosity, but are 2 mm. long; the anterior one is spatulate, somewhat emarginate, 4 mm. long, pilose at the base and on the middle line, otherwise glabrous. The flower is greenish-yellow; the anterior lobe violet.

"The species belongs near the very large leaved *V. grandifolia* Guerke and *V. bipindensis* Guerke, but differs in the squarrose, very loose inflorescences, and also in the remarkably numerous lateral veins of the leaves. The plant is certainly inhabited by ants, as one can conclude from the characteristic circular openings at the nodes of the branches" (Guerke, 1903).

Cameroon: Yaunde (Zenker).

ECOLOGY OF *Vitex Staudtii*

My attention was first called to this remarkable myrmecophyte by my friend, Mr. J. P. Chapin, at Avakubi, in January, 1914. Knowing my interest in ant-inhabited plants, he directed me to a swampy, wooded spot on the banks of the Ituri River, about five miles upstream from that locality, where there were many specimens of a creeper in the undergrowth of the forest. When the stems of this plant were slightly touched or otherwise disturbed, large numbers of slender, reddish ants rushed out of the hollow stalks ready to attack. I later came across the same creeper on several occasions during my travels in the Ituri Forest, and it appears to be fairly common throughout that region. On the other hand, I never saw it along the Semliki River or in the primitive forest between Lake Kivu and the Lualaba.

All the specimens observed by me were growing in very moist places, usually in parts of the forest flooded after heavy rains. The older plants consist of a long, flexible, woody main stalk, about 15 to 20 mm. thick at the base, or occasionally more. This stem begins to

branch feebly and irregularly a short distance from the ground and climbs freely among bushes and low trees, sometimes to a height of 8 to 10 meters. Its upper part is much more abundantly ramified and spreads leaves and flowers over the crown of the supporting vegetation. The compound, digitate leaves, of three to five nearly sessile leaflets, are borne on long petioles and placed opposite each other in decussate rows. Young branches and those on the upper part of the plant are quadrangular their whole length, with four slightly convex or nearly flat sides and more or less winged angles. These four winged ribs are continuous along the limb, at the nodes running on both sides of the petioles. Older branches show the ribs much less pronounced, the surfaces between becoming more convex, but often they still possess fairly pronounced wings, which can even be traced along the main stalk. Stem and branches show no sign of swellings. I have never seen the flowers, but the fruit is small, spheroidal, dry, hard, and of a pale orange-yellow color when ripe.

Adult plants were always inhabited by ants, invariably of the species *Viticicola tessmanni* (Stitz). The insects enter and leave their nests through a few orifices arranged in pairs at the nodes, nearly opposite each other and between the points of insertion of the leaves (Fig. 88a). The aperture, usually more or less crater-shaped, is placed at the top of a slight elevation which is produced by a peculiar ring of sclerenchyma, as shown by Prof. Bailey (see Part V, p. 591). On examining a very young specimen of this *Vitex* still free of ants, I was unable to find a depression, elevation, or scar on the surface to indicate the points where the insects would later gnaw entrance holes. Prof. Bailey's histological study shows that the most favorable situation for the nodal apertures is midway between the points of attachment of the leaves (see Part V, p. 592). The location of exits in *Vitex Staudtii* compares to a limited extent with that in *Cecropia adenopus*, in which, however, the entrances are always pierced above the axils of the leaves but in a section of the stem which is practically devoid of tough tissues (Schimper, 1888). In *Cecropia* the location of this diaphragm of softer tissues is marked externally by a roundish depression or prostoma, at the upper end of a shallow groove running upward from the insertion of the petiole; the ants of *Cecropia* always locate the entrance to the hollow stems in the depressed prostoma. How in *Cecropia*, *Vitex Staudtii*, and other similar cases the ants discover the spots particularly favorable for apertures and why they practically restrict their attacks to these parts of the stem are questions which cannot be satisfactorily answered at present. It

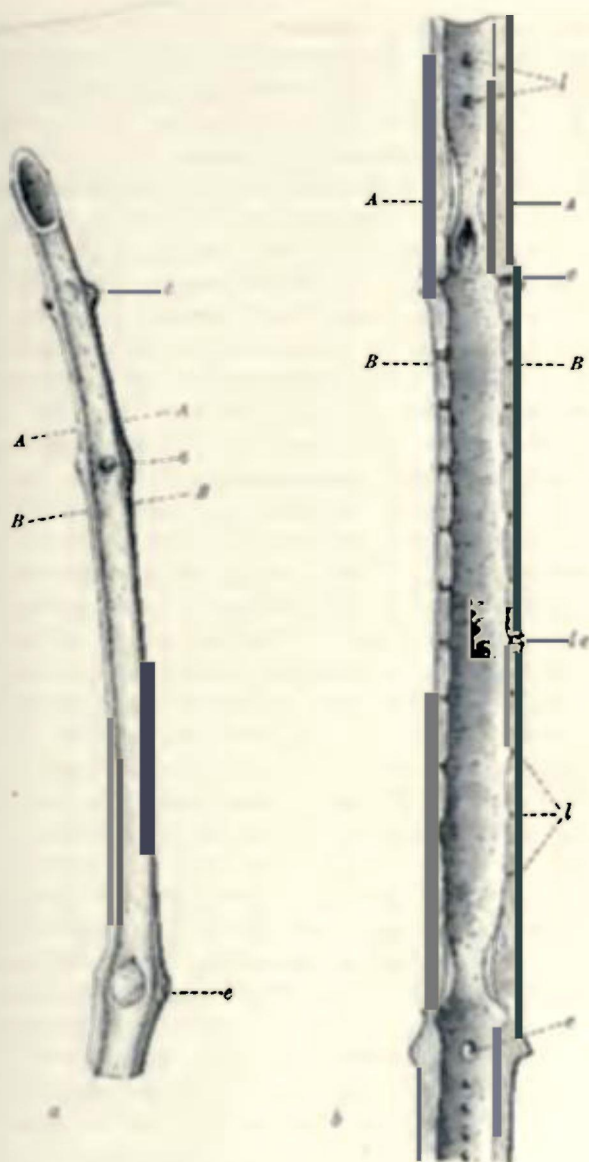


Fig. 55. *Vitis Staudtii* Guerke: a, external view of portion of stalk inhabited by the ant *Viticollela trumanni* (Stitz); b, longitudinal section of an older stalk; e, entrances to cavities at nodes; l, lateral galleries excavated by ants through the xylem and ending blindly beneath the bark; lc, accessory exit where one of the lateral galleries was gnawed through the bark. The lines A-A and B-B indicate the levels from which cross sections are figured in Pl. XXX, fig. 1 (A-A) and fig. 2 (B-B). Drawn from life at Avakubi, January, 1914; natural size.

has been suggested (Wheeler, 1913, p. 136) that ants may be able, through their extremely delicate tactile (or rather chordonotal) sense-organs, to select the thinnest spot in the wall of a cavity for perforation. Their sense of smell may also warn them against gnawing parts of the stem containing certain distasteful substances.

A longitudinal section of the stalks (Fig. 88b) discloses many features of further interest. In the first place, adult plants occupied by an ant colony are hollowed out nearly from top to bottom, all the internodes and various branches freely communicating with one another. The entire plant shelters one ant community, containing, in addition to one or more dealated queens, a number of fertile, ergatoid, wingless females. The formicaries of *Viticicola tessmanni* in the stems of *Vitex Staudtii* are thus splendid examples of polygynous insect societies. As in the case of *Pachysima* colonies in *Barteria*, they probably originate through secondary pleometrosis, or subsequent fusion of several isolated colonies, each started by a fecundated queen in the various limbs. A young specimen of *Vitex Staudtii*, scarcely 1 m. high, growing near the village of Nduye, between Penge and Irumu, was particularly instructive in this connection. Each of the lower internodes on the side-branches was occupied by a fertile, dealated female of *Viticicola tessmanni*, together with brood at various stages of development; no workers were present.

The ants clean out most of the medullary tissue nearly the entire length of the internodes, leaving only a peripheral layer of it for a short distance a little above the node. This remaining pith partly constricts the cavity and is probably left to keep the brood of the ants from dropping below the node, thus helping to distribute it regularly over the various internodes of the vertical stems and also preventing it from obstructing the apertures at the nodes. On a level with this inner circle of tissue the walls of the stem are also slightly thicker than in the other parts of the internode. At Kilo, in June, 1914, I saw a very young *Vitex Staudtii* composed of an unbranched, leaved, erect, thin stem about two feet high and unoccupied by ants. The central cylinder of the whole plant was filled with soft medullary tissue. It is possible that this substance dries up by itself, causing the stems to be hollow without the intervention of ants. In nature, however, this must be rarely the case, for, in adult plants housing a colony of *Viticicola*, pith is found only in the topmost internode of very young branches which are still green and soft; the ants steadily work upward through the nodes and excavate the interior before it has begun to dry.

The inner walls of the hollow stalks also show a peculiar series of depressions or narrow channels, the like of which is not known for any other myrmecophyte. These lateral cavities perforate the xylem and end blindly just under the cambium; they are arranged at irregular intervals, one above the other, in two longitudinal rows. The rows are opposite each other and their position shifts at every node, so that they always run on the sides corresponding with the upper pair of apertures of every internode. The number of channels in a row varies with the length of the internode, in some cases there are fifty or more, but often fewer. It occasionally happens that one of these lateral galleries perforates the bark, and this supplementary exit hole then produces the same projecting ring of sclerenchyma which surrounds the normal, crater-like apertures at the nodes. Since no trace of lateral cavities is found in young internodes where the pith has not yet been removed by the ants, we must conclude that they are excavated by the workers of *Viticicola*. They are not used by the inmates for their eggs or very young larvæ. Coccids are not found in these channels and, furthermore, are absent from the hollow stalks of *Vitex Staudtii*. It was at first believed that the channels assist in the aeration of the hollow interior, but this is disproved by Prof. Bailey (see Part V, p. 586). He found that the bark outside the depressions presents no lenticels or patches of aerenchyma for the exchange of gases. On the contrary, the overlying tissues are compact and, in old stems, there are disks of impervious sclerenchyma located just opposite the blind ends of the cavities. Moreover, Prof. Bailey discovered that the channels are not natural gaps in the woody portion of the wall, but are excavated by the ants in peculiar cores of delicate, unligified cells, that are symmetrically distributed in certain radii of the stem and surrounded by abnormal tissues similar to those presented by heteroplasmatic zoococcidia. The arrangement of the galleries in two rows below the apertures of the upper node results from the fact that in *Vitex Staudtii* the principal water-conducting passages in each internode are largely confined to those sides of the stele which pass out to the leaves at the next (higher) node. The lateral cavities are excavated in the sides of the stele poorly supplied with vessels and, furthermore, located in those portions of the xylem which are devoid even of a narrow fringe of small primary tracheæ.

Prof. Wheeler has given a detailed description of *Viticicola tessmanni* (Stitz), the obligatory guest of *Vitex Staudtii*, in its various adult phases and larval stages. My observations in the field furnish no clue as to the possible food of these insects, but the ants are evidently adapted

to their life within the cavities. Owing to the fact that the plant grows in swampy places, I am inclined to believe that the ants seldom, or never, leave their host. Wheeler and Bailey's examination of food-pellets dissected from the infrabuccal pockets of the adults and the trophothylaces of the larvæ failed to reveal traces of food from an outside source. The insect substances in the pellets of the larvæ resembled the yolk of ants' eggs and the fat-body of the larvæ themselves, suggesting that some of the brood had been used as nourishment for the more vigorous progeny. In one instance pieces of the skin of a *Viticicola* larva could be clearly recognized. There were also spores and bits of hyphæ in many cases and particles that seemed to be pith and callus tissue (Wheeler and Bailey, 1920, p. 261). Bailey thinks that the principal food of *Viticicola tessmanni* is provided by the medullary tissue of young twigs and the "nutritive layer" which is produced in the lateral galleries of the domatia (see Part V, p. 606).

Viticicola tessmanni is exceedingly vicious and alert. When its host plant is ever so slightly disturbed, the workers rush out of the hollow stalks in large numbers and actively explore the plant. Their sting is extremely painful and sometimes produces vesicles on the skin. It is certain that they constitute a very efficient body-guard of their host. Yet, on one occasion, I observed galls on the leaves of a *Vitex* occupied by the ants.

Rubiaceæ

In Africa, as elsewhere, this family is the richest in myrmecophytes, and without doubt the list of its species which form cœnobiotic associations with ants will be considerably increased by future investigation. Unfortunately many of the genera contain a large number of closely allied forms and even the generic distinctions are often unsatisfactory. It is, therefore, urgent that field-observations on these plants be accompanied by complete and abundant herbarium specimens for later identification by botanical experts.

So little is known about the two following cases that I have not treated them in the same detail as true myrmecophytes.

Grumilea venosa Hiern

Grumilea venosa HIERN, in Oliver, 1877, 'Flora of Tropical Africa,' III, p. 217. DE WILDEMAN AND DURAND, 1901, 'Reliquie Dewevreane,' p. 130. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 280. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 167.

Specimens collected by Dewevre in the Belgian Congo (Leopoldville; Bokakata) bear the following note: "Arbuste de 2 m. environ, toujours habite par de nombreuses fourmis noires." (De Wildeman and Durand, 1901, p. 130).

Uragoga species ?

In the forest bordering one of the affluents of the Congo near Leopoldville, I came across a semiberbaceous, low bush, which I provisionally refer to the genus *Uragoga* (May 18, 1915; Coll. No. 7656). The flowers are white, with greenish spots on the teeth of the corolla; the fruit is a red berry. At each node, between the points of attachment of the leaves, there are two curious, persistent stipules, occupying the entire width of the stem (Fig. 89). They are convexly swollen to the upper side and the free margin is recurved downward, the whole forming an inverted cup or pouch broadly open below. Coccids were usually found inside this cavity and the ants, *Crematogaster striatula* variety *obstinata* (Santschi), had built a tent of vegetable material over the inferior opening of the stipules. I did not find eggs, larvæ, or pupæ of these ants inside the stipules, which I therefore regard not as myrmecodomatia but merely as "kraals" to shelter the scale insects. Yet this case suggests useful comparison with the stipular pouches of *Macaranga saccifera* and other more typical ant structures of plants.

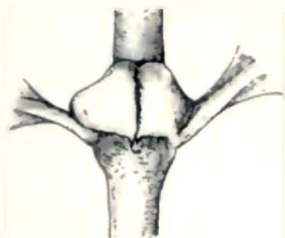


Fig. 89. *Uragoga* species? Swollen stipules at base of a stem of leaves; drawn from life at Leopoldville, May, 1915; twice natural size.

UNCARIA Schreber

Uncaria SCHREBER, 1789, in Linnaeus, 'Gen. Plant.,' Ed. 8, I, p. 125. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 41. HAVILAND, 1897, Journ. Linn. Soc. London, Botany, XXXIII, p. 73.

Ouroparia AUBLET, 1775, 'Histoire des Plantes de la Guiane française,' I, p. 177, Pl. LXVIII. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 57.

Agulophora NECKER, 1790, 'Elementa Botanica,' I, p. 145.

Climbing shrubs with opposite, interpetiolar, fugacious stipules; the lower part of the terminal branches with axillary recurved hooks, often spirally rolled up and placed opposite each other; in some cases these hooks still bear a few aborted, opposite leaves. On older branches the recurved hooks are often replaced by heavy, woody thorns. Leaves usually leathery, rarely herbaceous; the stipules entire or bifid. Flowers pedicelled or sessile, crowded into loose, globose heads, without intervening bracteoles. Flower heads placed in the axils of the upper leaves, either singly or in decussate panicles. Calyx salver-, or bell-, or funnel-shaped; the calyx-tubes

not cohering, finally fusiform; the limb campanulate, 5-lobed or 5-partite. Corolla often silky outside, funnel-shaped with an elongated tube; the lobes overlapping one another in the bud; throat of the tube bare. Stamens 5, inserted at the throat of the corolla; filaments short; anthers short oblong, the theca more or less extended or in some species setose at the base. Disk inconspicuous. Ovary fusiform, 2-celled; style exserted far beyond the tube of the corolla, ending in a clavate or capitate stigma. Ovules numerous, ascending, inserted on a placenta which is borne by the middle partition of the ovary. Fruit a septicidal, many-seeded capsule; testa of the seeds extended at both ends into capillary appendages.

Uncaria is a close relative of the East Indian *Nauclea*, differing mainly in the characters of the fruit, which in the last-named genus is a capsule, not septicidal, but merely breaking up into two cocci or lobes. All the species of *Uncaria* are climbing shrubs found in the forested areas of the tropics. Over thirty species are known, most of them from tropical Asia; two occur in South America and one in Africa.

Uncaria africana G. Don

Uncaria africana G. DON, 1834, 'General System of Gardening and Botany,' III, p. 471. HOOKER, 1848, 'Icones Plantarum,' VIII, Pl. DCCLXXXI. BENTHAM, 1849, in Hooker, 'Niger Flora,' p. 381, Pl. XLII. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 41. HAVILAND, 1897, Journ. Linn. Soc. London, Botany, XXXIII, p. 76. E. DE WILDEMAN AND T. DURAND, 1900, Bull. Herbar Boissier, (2) I, p. 25; 1901, 'Reliquiæ Dewevreanæ,' p. 106. E. DE WILDEMAN, 1903, 'Études Flore Bas- et Moyen-Congo,' I, p. 76; 1907, *ibid.*, II, pp. 71 and 192. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 241. E. DE WILDEMAN, 1910, 'Études Flore Bas- et Moyen-Congo,' III, pt. 2, p. 283; 1912, *ibid.*, III, pt. 3, p. 484.

Nauclea africana WALPERS, 1843, 'Repertorium Bot. Syst.,' II, p. 512 (*nec* Willdenow).

Ouroparia africana BAILLON, 1879, Bull. Soc. Linn. Paris, I, p. 228. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 57. HIERN, 1898, 'Catalogue Afr. Plants Welwitsch,' II, p. 435.

Uruparia africana K. SCHUMANN, in Engler, 1895, 'Pflanzenwelt Ost-Afrikas,' C, p. 378.

"A glabrous or sparingly pubescent shrub 4 to 40 ft. high. Leaves ovate-oval or lanceolate, acuminate, rounded at the base or nearly so, thinly coriaceous, with 5 to 7 lateral veins on each side of the midrib, shortly petiolate, 2 to 6 by 1 to 4 in.; stipules $\frac{1}{4}$ to $\frac{1}{3}$ in. long, usually bipartite with narrow partitions. Spines at first nearly straight, afterwards crooked. Flowering heads $1\frac{1}{2}$ to 2 in. in diameter. Calyx tawny, as well as the corolla shortly and appressedly pilose-tomentose; limb shortly lobed. Corolla about $\frac{1}{2}$ in. long, greenish yellow. Stamens glabrous; anther-cells obtusely produced at base. Fruiting heads 3 to $3\frac{1}{2}$ in. in diameter; pedicels $\frac{3}{4}$ in. long; capsules $\frac{3}{4}$ in. long. Tails of the seeds linear-setaceous, undivided at one end, bipartite at the other" (Hiern, 1877).¹

¹Haviland's diagnosis reads: "Frutex 1-15-metr. Ramuli glabri vel pubescentes; internodi 7-9 cm. Folia 13 cm. longa, 6 cm. lata, elliptico-lanceolata, longe acuminata, supra glabra, subtus glabrescentia, nervis 7-8. Petioli 7 mm. Stipulae bifidae, lobis acutis. Pedunculi 7 cm., maxime variabiles. Flores pedicellati vel subsessiles. Corolla sericea, mellea; tubus 1 cm., lobi oblongi. Calyx sericeus; tubi pars superior 4 mm.; lobi 1 mm., obtuse triangulares. Stylus 18 mm.; stigma 4 mm., elongato-clavatum. Capsulae 2 cm., cum pedicellis aequilongae. Bractea nulla."



Fig. 90. *Uncaria africana* G. Don. Extremity of branch with capitulum of fruits (after Bentham, 1849).

Sierra Leone, type locality (G. Don; Afzelius; Barter; Scott Elliot; Johnston).
Nigeria (Vogel).

Cameroon.

Spanish Guinea: Rio Muni (Mann).

Belgian Congo: Lower Congo: banks of the Lukungu River (Dewevre); Kisantu (Gillet); Inkisi River (Vanderyst). Kasai: Linkanda (Gentil). Upper Congo: Mondombe (Jespersen). Northeastern Congo forest: Mangbetu Country (Schweinfurth); Uele region (Seret); Barumbu (November 3, 1913; J. Bequaert; Col. No. 1669); Penge (January 27, 1914; J. Bequaert; Coll. No. 2136); between Penge and

Irumu (village of Tete, February 22, 1914; J. Bequaert; Coll. No. 2658); between Walikale and Labutu on the Oso River (village of Mandimbo, January 18, 1915; J. Bequaert; Coll. No. 6664).

Uganda.

Angola: Colungo Alto "in the primitive forests of Sobato de Mussengue" and "in the very dense, primitive forest of Quibanga" (Welwitsch).

Also known from Madagascar and the Comoros.

Haviland distinguishes several varieties:

Variety (1). Flowers subsessile. Upper part of the calyx-tube 4 mm. long. Sierra Leone, Niger, Mangbetu.

Variety (2) *madagascariensis* (*Ourouparia madagascariensis* Baillon, 1879, Bull. Soc. Linn. Paris, 1, p. 228). Flowers subsessile. Upper part of the calyx-tube 2 mm. long. Malagasy Region.

Variety (3) *angolensis* Haviland. Flowers pedicellate. Upper part of the calyx-tube 4 mm. long. Angola.

Variety (4). Flowers pedicellate. Upper part of the calyx-tube 2 mm. long. Cameroon.

The variety *angolensis* Haviland is described more in detail by Hiern (1898) as follows:

An arborescent shrub, glabrous except the inflorescence. Trunk in some cases more than 100 ft. long and 6 in. in the lower part, climbing to a very great height and then hanging down; branches patent, fuscous, rather glossy, tetragonal. Leaves opposite, elliptical, narrowly acuminate at the apex, obtusely narrowed or nearly rounded at the base, thinly coriaceous, glossy, dark green above, paler beneath, 2 to 4 1/2 in. long, 1/2 to 1 3/8 in. broad; lateral veins about 6 on each side of the midrib, slender; petiole 1/8 to 1/4 in. long. Stipules ovate, small, somewhat hairy on the inner face, nearly deciduous. Spines axillary, mostly crooked, 1/4 to 3/4 in. long. Flower heads terminating the branches, shortly pedunculate, globose, about 2 in. in diameter. Flowers golden-tawny, about 3/4 to 7/8 in. long (including the exerted style), very numerous, crowded. Pedicels about 1/8 to 1/6 in. long in flower, 3/8 in. long in fruit, tomentellous. Bracts 0. Calyx silky-tomentellous with short upward hairs, somewhat constricted above the ovary, greenish-fuscous; tube broader than the ovary, campanulate, funnel-shaped, 1/6 to 1/5 in. long, shortly 5-cleft, lobes thickly lanceolate. Corolla 1/2 to 3/5 in. long; tube slender, except the base clothed outside with downward tawny short silky-tomentose hairs, 1/2 in. long; limb much broader than the tube, hemispherical, 1/5 to 1/4 in. in diameter, golden-tawny tomentose outside, glabrous inside, deeply 5-lobed; segments about 1/8 in. long, obovate-oblong, rounded at the apex with an apiculus. Stamens 5, about half as long as the corolla-lobes, glabrous, introrse, inserted on short, flattened filaments at the base of the corolla-limb. Ovary ellipsoidal, tomentose, rather thicker than the base of the calyx-limb, much thinner than the top of the calyx-limb. Style filiform, exerted about 1/4 in. beyond the corolla, glabrous below, stigmatose and rather thickened in the upper part towards the clavate stigma. Young fruit subglabrous, about 3/8 in. long, 1/6 in. thick, narrowed at both ends especially towards the base.

This species probably occurs throughout the African Rain Forest. In a recent note, De Wildeman (1919) calls attention to the myrme-

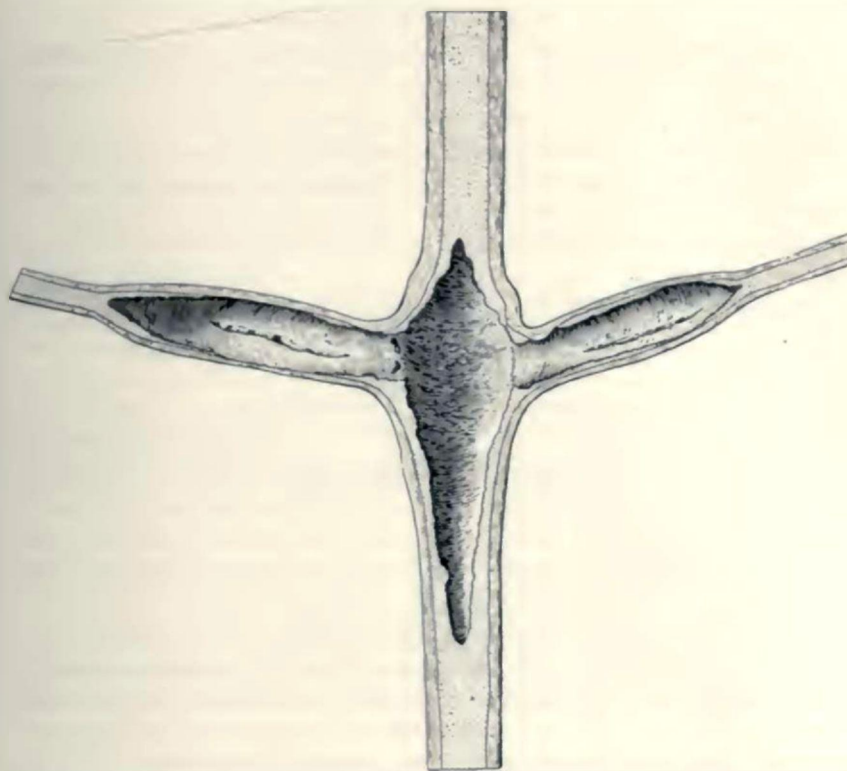


Fig. 91. *Uncaria africana* G. Dou. Longitudinal section of myrmecodomatium at a node, showing three cavities communicating with one another; the aperture is not figured. Drawn from life at Barumbu, November, 1913; natural size.

copytism of certain African plants of this genus. He proposes, provisionally, the varietal name *myrmecophyla* De Wildeman for specimens which I collected in the Ituri Forest at Penge and between Penge and Irumu, without, however, giving characters by which this new variety could be differentiated from the typical form. I am inclined to believe that myrmecophytism is normal for *Uncaria africana* throughout its range and has merely been overlooked thus far. When terminal branches alone are collected, there may be no indication of the peculiar myrmecodomatia in herbarium specimens, even should such have been present on lower parts of the plant. Ant-inhabited parts of plants are also frequently avoided by botanical collectors. Moreover, it is possible that the myrmecodomatia are absent or but little pronounced in certain individuals or at certain stages of growth.

ECOLOGY OF *Uncaria africana*

Here (Figs. 90 and 91) we have one of the many climbing bushes or "scramblers"—as Schimper proposed calling them—which frequently form tangles of vegetation over the low trees at the edge of clearings and along river banks. While the trunk and main branches are straight and stiff as in ordinary bushes, all or part of the lateral branches are limp and pliable. The latter either hang down freely or work their way upward, keeping hold of the other trees by means of the spirally curved hooks and woody thorns, which are placed in pairs above the nodes and are evidently modified branches. The leaves are glabrous, as well as the branches at the extremity of some of which the flowers or fruits form head-clusters.

The myrmecodomatium of this *Uncaria* consists of the enlarged and hollow basal internodes of two opposite, lateral branches, the cavities in this pair of swellings communicating with the hollow, very slightly swollen node of the main branch (Fig. 91). The middle chamber is more or less club-shaped, 5 to 6 cm. long and 10 to 20 mm. wide in the upper half; it is dug farther into the pith below than above. The two lateral cavities are 3 to 6 cm. long and 6 to 10 mm. broad.

All the specimens I had opportunity to study in the field were inhabited by ants of the genus *Crematogaster*, which were identified as *C. excisa* subspecies *andrei* (Forel) in the case of the plants found near the Oso River, between Walikale and Lubutu in January, 1915. The myrmecodomatia contained not only the queen, workers, and brood of the ants, but also numerous coccids. These scale insects were invariably located in the lateral swellings and fixed at the bottom of two deep, opposite, longitudinal grooves in the inner wall. One or more circular exit holes are pierced by the ants through the sides of the lateral cavities. Often the depressions occupied by the coccids are open to the exterior by means of irregular slits through which the ants enter and leave. It would thus seem that these grooves are gnawed by the ants, probably on account of some special hyperplasias formed in that region of the walls. The coccids merely select the grooves for nutritive, juicy tissue to be found there and continually renovated by the attacks of the ants.

On the plants examined by me at Barumbu in November, 1913, there were a number of young branches whose basal internodes, though distinctly swollen, were still filled with juicy pith tissue. In another instance, between Walikale and Lubutu, the basal swellings of many older branches were not yet inhabited by ants, presenting no exit holes; nevertheless, they were entirely hollow inside, so that the cavities of

Uncaria originate through the drying up of the pith and without the agency of ants, as I have shown to be the case with the myrmecodomatia of *Barteria fistulosa*.

SARCOCEPHALUS Afzelius

Sarcocephalus AFZELIUS, 1818, in R. Brown, Tuckey's 'Narrative Exp. Zaire,' Appendix No. 5, p. 467. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 38. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 58.

Trees or shrubs with subterete or obtusely quadrangular branches and opposite, subcoriaceous, petiolate leaves (rarely in whorls of three). Stipules interpetiolar and deciduous in the African species, often very large. Flowers whitish, pale pink or yellowish, crowded on globose, common receptacles, forming compact, pedunculate, globose, terminal and axillary heads, without intervening bracteoles. Peduncles of the flower heads with small bracts below the middle. Calyx-tubes cohering, truncate or with 4 or 5 teeth; these teeth hairy, jagged at the tip or in some species with as many alternating appendages. Corolla narrowly funnel-shaped, with glabrous throat, rather fleshy, glabrous or pubescent, 4- or 5-lobed, imbricated in prefloration, deciduous. Anthers 5, subsessile, inserted at the mouth or throat of the corolla, ovate-oblong. Disk inconspicuous. Ovaries grown together, 1- or 2-celled. Style filiform, exerted far outside the corolla, caducous. Stigma oblong or spindle-shaped, thicker than the style, glabrous, entire, emarginate, or bifid. Placentas centrally attached (in the African species). Ovules numerous, anatropous. Syncarpium fleshy, globose, pitted or uneven, its cells with thin walls and divided by membranaceous septa. Seeds small, not winged, ovoid, and placed above one another (in the African species); funicles spongy; testa crustaceous; albumen fleshy.

The members of this genus are usually easy to recognize in the field, especially when in fruit. Haviland in his monograph of the *Nauclea* (1897) recognizes thirteen species in the tropical regions of the Old World. The number of described forms has been considerably increased in later years and must now approximate thirty. Of these six are recorded from Africa and four from the Belgian Congo.

According to K. Schumann (1891b, p. 59), *Sarcocephalus macrocephalus*, from the Philippines, has swellings inhabited by ants. Haviland is inclined to believe that the plant in question was a *Nauclea*, a genus known to contain several myrmecophytic species in the Philippines. In the Belgian Congo, however, there is a true *Sarcocephalus* with myrmecodomatia. At present I can not give its specific identity, but it is certainly very distinct from the common *S. sambucinus* (Winterbottom), = *S. esculentus* Afzelius, which, according to my observations, is never inhabited by ants. Most probably it represents a distinct, undescribed form.

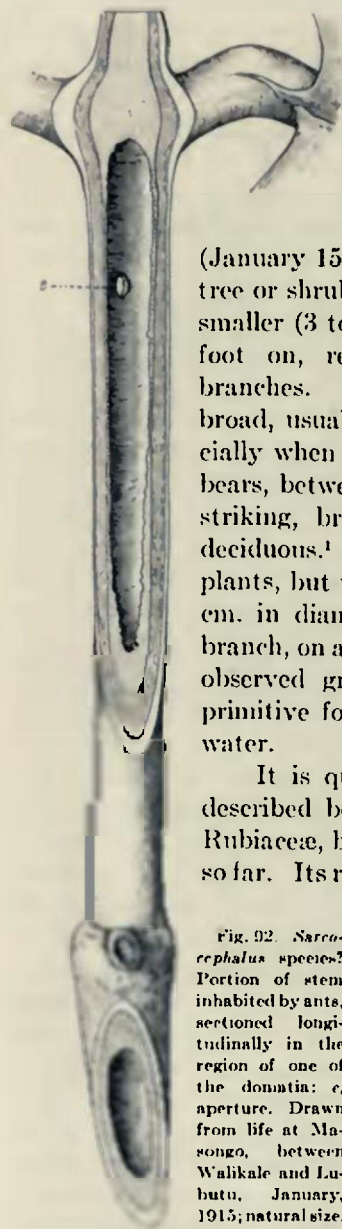


Fig. 92. *Sarcocephalus* species? Portion of stem inhabited by ants, sectioned longitudinally in the region of one of the domatia: c, aperture. Drawn from life at Masongo, between Walikale and Lubutu, January, 1915; natural size.

ECOLOGY OF *Sarcocephalus* SPECIES

This myrmecophyte was first met with in the Ituri Forest, near the village of Banana between Penge and Irumu (February 24, 1914; Coll. No. 2605) and was again seen near the village of Masongo, between Walikale and Lubutu (January 15, 1915; Coll. No. 6629). It is a low, erect tree or shrub, rarely over 8 meters high, usually much smaller (3 to 4 m.). The straight trunk bears, from its foot on, regularly spreading, opposite, decussate branches. The leaves are opposite, large and very broad, usually purplish-red on the under side, especially when young. The terminal part of the branch bears, between the points of attachment of the leaves, striking, broad stipules which, however, are early deciduous.¹ It never happened that I saw flowering plants, but the fruit is a spheroidal, solid ball, 9 to 10 cm. in diameter, placed at the extremity of a side branch, on a short, recurved pedicel. All the specimens observed grew on swampy, rather open spots of the primitive forest, either at the edge of a brook or in the water.

It is quite possible that this species has been described before, perhaps under a related genus of Rubiaceae, but it agrees with none of the diagnoses seen so far. Its relation with ants would easily escape notice, for the myrmecodomatia are inconspicuous and, when not actually occupied by insects, could often be discovered only upon sectioning the branches. Externally, they consist (Fig. 92) of a very slight, often imperceptible swelling on the upper half or two-thirds of the internode. Inside, the central cylinder is hollowed out into a spacious cavity, 6 to 8 cm. long and 5 to 7 mm. wide at the top. Domatia inhabited by ants have a circular aperture a short distance below the node.

¹In the common African *Sarcocephalus sambucinus* the stipules are small (4 mm. long) and persistent; but they are large and caducous in many other species of the genus.

Sections made of a number of young specimens of this myrmecophyte not yet settled by ants showed that in this case, too, the swollen upper portion of the internodes becomes hollow of its own accord through the drying up of part of the medullary tissue; such cavities have no exit holes. In this species the lower internodes of the main trunk and side branches are neither transformed into domatia nor in the least swollen and remain completely filled with pith. Very young plants show no trace whatsoever of ant-chambers and on an adult tree the size and shape of the myrmecodomatia becomes more pronounced toward the upper branches.

In both localities where I observed this *Sarcocephalus* a number of specimens were inhabited by small ants of the genus *Crematogaster*. Those taken from the domatia of the plants between Walikale and Lubutu were identified by Santschi as *C. africana* subspecies *winkleri* variety *fickendeyi* (Forel), a form commonly found nesting in other places. These insects had established regular colonies in the cavities, with a queen, workers, and brood; coccids were also among them, fixed on the inner walls.

RANDIA Linnæus

Randia (Houston) LINNÆUS, 1753, 'Species Plantarum,' Ed. 1, II, p. 1192. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 93. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 75.

Erect or scandent, spinous or unarmed shrubs or trees, with opposite or verticillate, often leathery leaves; stipules rather short, solitary, entire, more or less heath-like. Flowers large or medium-sized; solitary, few together, or corymbose; as a rule apparently axillary or terminating short lateral branches, or terminal. Calyx-tube ovoid or turbinate, ribbed or cylindrical; the limb usually tubular, truncate, toothed, lobed, or spatheous; lobes sometimes foliaceous. Corolla white or yellowish, or more greenish; campanulate, funnel-shaped, or salver-shaped; tube in some species much elongated; limb spreading or reflexed, dextrorsely contorted in the bud. Anthers sessile or subsessile, narrowly linear, inserted at or near the throat or mouth of the corollar tube, included or exerted. Disk annular or cushion-shaped. Ovary 2-celled. Ovules very numerous, immersed in the fleshy placentas. Style strong, glabrous or hairy; stigma club- or clapper-shaped, entire, bidentate or bilobed, sulcate. Berry 2-celled, usually many-seeded; the testa of the seed leathery or membranous.

This genus is close to *Pouchetia* A. Richard and *Oxyanthus* de Candolle; still more so to *Gardenia* Ellis, which it often resembles in general habitus. *Gardenia* has the ovary completely one-celled for the whole length; this character, however, is not always easy to decide upon because in certain species of *Randia*, as, for instance, *R. physophylla*, the ovary is incompletely divided into two cells.

About 150 species have been described, by far the majority being found in the Oriental and Ethiopian Regions and a few in Tropical America. In the Belgian Congo the genus is well represented by some twenty-five species. They are trees or bushes with large, showy flowers, growing mostly in the Rain Forest or in the forest galleries along the streams of the Savannah.

Three of the African species are associated with ants; they all belong to that section of the genus in which the lobes of the calyx are elongate, slender, subulate, and not leaf-like. *R. physophylla* K. Schumann is characterized by the presence of glandular cavities at the base of the leaf-blade (Fig. 94). The two others, *R. myrmecophyla* E. De Wildeman and *R. Lujæ* E. De Wildeman, possess caulinary myrmecodomatia and, in addition, agree in the following characters:

Trees or shrubs with glabrous branches, feebly flattened at the nodes; the internodes often swollen, spindle-shaped; the swellings being hollow, usually pierced by one or more orifices and inhabited by ants; the leaves are opposite, or apparently verticillate, three of them being placed at about the same level; blade obovate, acuminate, constricted at the base into a rather thick, short petiole.

They can be separated as follows on characters mentioned in their descriptions:

Flowers erect, placed by twos or fours in the axils of the leaves, about 22 cm. long; tube of the corolla glabrous externally. Leaves smaller, with acarodomatia in the axils of the lateral veins. *R. Lujæ* De Wildeman.
Flowers pendent, solitary, terminal, much larger; the corolla alone 22 to 25 cm. long, shortly tomentose externally. Leaves larger, the blade as much as 30 cm. long and 15 cm. broad, without acarodomatia. *R. myrmecophyla* De Wildeman.

Randia Lujæ De Wildeman

Randia Lujæ E. DE WILDEMAN, 1901, C. R. Ac. Sci. Paris, CXXXVIII, p. 914; 1901, 'Notices sur des Plantes utiles ou intér. Flore du Congo,' I, pt. 2, pp. 282-284; 1907, 'Études Flore Bas- et Moyen-Congo,' II, p. 159; 1910, *ibid.*, III, pt. 2, p. 286; 1912, *ibid.*, III, pt. 3, p. 487. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 259. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 155 and 158. E. DE WILDEMAN, 1920, 'Mission de Brier au Mayumbe,' pp. 43, 88, 222, and 264.

"Large tree with glabrous branches, the internodes often thickened toward the base and pierced by one or two orifices leading into a cavity inhabited by ants. Leaves obovate, acuminate, narrowed at the base into a short and rather thick petiole; blade rather coriaceous, darker colored above than below, 20 to 25 cm. long, 5 to 12 cm. broad, glabrous on both sides, with an acumen of 15 mm. Lateral veins numbering about 9 on each side of the midrib, anastomosing into a curve before reaching the margin, little or not prominent above, prominent on the under side; in the axils of the origin of the lateral veins there are acarodomatia excavated in the tissue of the nervure and opening by a pore at the under side of the blade, more or less visible on

the upper side as feeble swellings. Flowers by twos, erect, sessile or subsessile, about 22 cm. long; calyx about 17 mm. long, glabrous, with 5 ribs ending in 5 subulate, irregular teeth; corolla with a long linear, glabrous tube, rather abruptly widening in its upper part, the broadened portion about 22 mm. long; ending in 4 ovate-lanceolate, acute lobes of about 3 mm.; glabrous externally, sparsely villous internally. Stamens partly exerted, extending beyond the broadened funnel of the corolla for about 11 mm. Fruit globose, voluminous, over 15 cm. in diameter" (E. De Wildeman, 1904).

Belgian Congo: Kasai: forest along the Sankuru River, type locality (Luja). Middle and Upper Congo: Lukolela (Claessens); Lokelenge (Bruneel); Bianga (Beliefroid). Mayombe: Ganda Sundi (de Briey).

According to De Wildeman (1910, p. 286) the leaves are often placed in verticils of three; the flowers frequently by fours; the fruit is grayish, subspherical, with 5 more or less conspicuous ribs. This species is close to *Randia maculata* de Candolle, = *R. longiflora* (Salisbury), but differs in the presence of acarodomatia in the axils of the lateral veins and the ant-swellings of the internodes.

Randia myrmecophyla De Wildeman

Randia myrmecophyla E. DE WILDEMAN, 1907, 'Etudes Flore Bas- et Moyen-Congo,' II, pt. 2, p. 160, figs. 5-8, Pls. xxxviii-xxxix; 1908, *ibid.*, II, pt. 3, p. 346; 1907, 'Mission Emile Laurent,' V, pp. cexxiii-cexxiv, figs. IX, XI.

Randia myrmecophila TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 260.

Randia myrmecophila H. KOHL, 1909, *Natur u. Offenbarung*, LV, pp. 158-160, fig. 5.

"Shrub with glabrous branches, which are flattened at the nodes, and swollen toward the apex of the more or less lengthened internodes. Internodes hollowed over part of their length, sheltering ants and coccids. Leaves opposite or pseudo-verticillate by threes, petiolate; the petiole flattened above. Stipules very broad, triangular, acuminate, about 4 mm. long. Flowers solitary, the calyx with 5 linear teeth. Corolla with a cylindric tube, widened in its upper part, with 5 lobes which are rounded at their apex. Anthers inclosed. Style with a club-shaped stigma, not or little exerted.

"Variety *typica* De Wildeman (1907, p. 160).

"Petiole 15 to 25 mm. long, short tomentose, flat above. Blade of the leaves cuneate at the base, rounded-cuneate at the apex, glabrous above, velutinous-tomentose on the under side, with 11 or 12 lateral veins on each side of the midrib, 20 to 40 cm. long and 9 to 13.5 cm. broad. Calyx short tomentose externally, becoming glabrous with age, densely villose and silky inside; its tube, including the ovary, about 2.5 cm. long, with conspicuous ribs ending beyond the truncate margin in 5 linear teeth, 5 to 13 mm. long. Corolla with its tube 22 to 25 cm. long, shortly tomentose externally; more heavily villose inside, except in its widened, glabrous part which is 9 cm. long; lobes villose on both faces, 5.5 cm. long and of about the same width, partly overlapping in the bud. Fruit ovoid, 10 cm. long, 8 cm. in diameter, with 5 feeble ribs.

"Variety *subglabra* De Wildeman (1907, p. 163).

"Petiole 8 to 15 mm. long, sparsely and short tomentose, flat on the upper side. Leaf-blade rather broadly cuneate at the base, glabrous and shiny above, glabrous and dull on the under side, except on the lateral veins of which there are 12 or 13 on each

side of the midrib; 18 to 23 cm. long and 7.5 to 12.5 cm. broad. Calyx short tomentose externally, becoming glabrous with age; densely silky-villose inside; its tube including the ovary about 2.5 to 2.8 cm. long, often split on one side; ribs conspicuous, ending beyond the truncate margin into 5 linear teeth, 16 mm. long. Corolla with a tube of 21 to 22 cm., the lobes about 4 cm. by 4 cm.; the villosity as in the form *typica*.

"Variety *glabra* De Wildeman (1907, p. 163).

"Petiole 15 to 30 mm. long, glabrous. Leaf-blade long cuneate at the base, glabrous on both faces, shiny above, dull below; with about 14 lateral veins on each side of the midrib; 18 to 26 cm. long and 6 to 10.5 cm. broad. Calyx glabrous externally; the tube including the ovary about 2 cm. long (in the bud), the teeth 6 to 15 mm. long" (De Wildeman, 1907).

Belgian Congo: Kasai: Bombaie (E. and M. Laurent). Middle and Upper Congo: Eala, type locality (Pynaert; M. Laurent; variety *typica*); Coquilhatville (M. Laurent; variety *subglabra*). Eastern Congo Forest: Yambuya (M. Laurent; Solheid; variety *subglabra* and variety *glabra*); Avakubi (January 13, 1914; J. Bequaert; Coll. No. 1917).

De Wildeman's figure of a flowering live plant (1907, p. 160, fig. 5) shows that the very large, solitary, terminal flowers are pendent. According to the same author, it belongs to the group of *R. malleifera* (Hooker), which species, however, differs in the absence of ant-swellings, the smaller corolla with much denser and longer tomentum on the tube, and the villosity of the stem.

Randia physophylla K. Schumann

Randia physophylla K. SCHUMANN, 1899, Engler's Bot. Jahrb., XXVIII, pt. 1, p. 64. É. DE WILDEMAN, 1903, 'Études Flore Bas- et Moyen-Congo,' I, p. 81; 1907, *ibid.*, II, pp. 74 and 164; 1912, *ibid.*, III, pt. 3, p. 487. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 260.

"Leaves very short petiolate or subsessile, oblong, short and sharply acuminate, broadly cuneate at the base, subcordate and auriculate below, the earlets excavated and glandular; leaves very glabrous on both sides, resinous and very shiny. Ovary, to judge from the fruit, globose, glabrous and scabrous. Calyx tubular and irregularly 5-lobed, the lobes costate and scabrous. Corolla pentamerous, each of the 5 lobes divided in the upper part into obovate, obtuse, carnosae laciniae. Anthers curved, broad. Style exerted for a long distance out of the corollar tube; subclavate and sulcate in its upper part. Berry globose, crowned by the calyx.

"The petiole is hardly 3 to 4 mm. long. The blade has a length of 30 to 35 cm. and a width in the middle of 12 to 14 cm.; it is crossed on each side of the midrib by 23 to 25 heavy lateral veins, which are visible on both upper and under surfaces; the leaf is shiny chestnut-brown in dried condition. The two semiglobose glandular cups at the base of the leaf are 5 mm. deep. The glands of the stipules must secrete an abundance of resin, for it fairly drenches the leaves and forms a crust at the base of the petiole. The calyx has a length of 3 to 3.5 cm. The corolla is very fleshy, 18 to 19 cm. long, of which 15 cm. is the length of the tube. The stamens are 1.3 cm. long. The style exceeds the corollar tube by about 3 cm. The berry has a diameter of 2.5 cm." (K. Schumann, 1899).

Cameroon: Grand Batanga (Dinklage); Bipindi (Zenker).

Belgian Congo: Lower Congo: Kisantu; Lukaya (Gillet); Sanda (Oddon); Kwango Region (Butaye); Leopoldville (April 15, 1915; J. Bequaert; Coll. No. 7317). Middle and Upper Congo: Ikela (Jespersen); Eala (M. Laurent); Lubi (Lesrauwaet).

ECOLOGY OF *Randia Lujæ*

The species was discovered by Lujæ in 1903 along the Sankuru River in the Belgian Congo. According to De Wildeman (1904a, pp. 282-284; 1904b) its myrmecodomatia are very similar to those of *R. myrmecophyla* described in detail below. They consist of spindle-shaped swellings of the internodes, about 2 to 3 cm. thick and hollow; one or two apertures, in the widest part of the swelling, lead into the cavity. There are, in addition, on the leaves, in the axils of the nerves acarodomatia in the form of small pouches. The ants found by De Wildeman in the domatia of *Randia Lujæ* have not been identified.

ECOLOGY OF *Randia myrmecophyla*

On only one occasion did I observe this species in the field. At Avakubi, in January, 1914, a specimen was found in the primitive Rain Forest, in a rather dry place. It grew as a bush with very broad and long, glabrous, smooth leaves; the blades were as much as 30 cm. long and 15 cm. wide and borne on a petiole sometimes 4 cm. long. The large, white, pendent flowers were very striking. The plant agreed perfectly in all particulars with De Wildeman's descriptions, photographs, and drawings of *R. myrmecophyla*.

The myrmecodomatia of this *Randia* (Fig. 93) are quite peculiar, being elongate, regular, spindle-shaped swellings on the middle portion of the internode, and extending about half its length. These expansions seem to occur in all the internodes of the various branches, usually present one circular aperture, occasionally two or three, near the middle of one side, and are inhabited by ants. A longitudinal section shows the interior of the enlarged part of the internode to consist of a spacious cavity, 10 to 12 cm. long and 6 to 7 mm. wide, which stops a long distance from the nodes.

The ants I found in the myrmecodomatia of the specimens at Avakubi belonged to a small species of *Crematogaster* recently identified by Santschi as *C. rugosa* (Andre). Each cavity apparently contained its own formicary with brood, and in many instances was divided into a series of chambers by transverse walls of brown, malaxated pith debris. Sometimes one hollow would thus be separated into four successive compartments communicating by one or two holes pierced through the

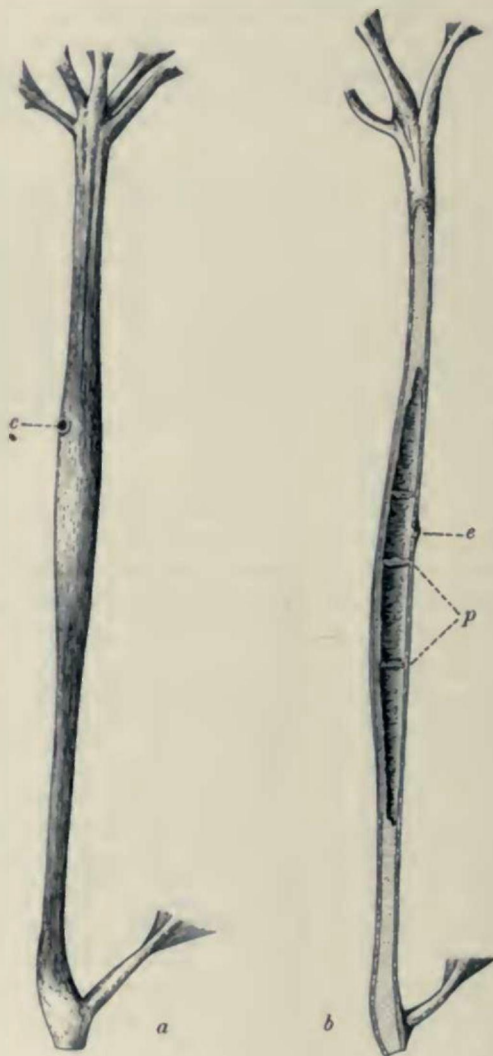


Fig. 93. *Randia myrmecophyla* De Wildeman: *a*, portion of branch showing swollen internode inhabited by ants; *b*, longitudinal section of this internode; *e*, entrance to cavity; *p*, partitions built by ants. Drawn from life at Avakubi, January, 1914; one-half natural size.

partitions; even then, there would usually be only one external aperture to the domatium. By means of these dividing walls the ants undoubtedly make a much more efficient use of the hollow internodes, for it has been observed that in such cases the larvæ and pupæ are kept toward the

nodes in the narrower upper and lower stories. Coccids are also common companions of the ants in this *Randia*.

Crematogaster rugosa is a small and timid ant and probably does not give its host much protection. Even when the branches containing formicaries are shaken, the inmates do not leave their retreats. The specimen near Avakubi, though settled by ants, had its leaves badly eaten by phytophagous insects.

Em. Laurent, the discoverer of this *Randia*, recognized its myrmecophily in the field. He found an unidentified ant and coccids in the swollen internodes. I am not aware that additional information on this plant has been published since, but Kohl in later years has collected from its domatia specimens of *Camponotus foraminosus* Forel and *Cataulacus ucissi* Santschi (Forel, 1916, pp. 427 and 443).

ECOLOGY OF *Randia physophylla*

I found a specimen of this species in a forest gallery near Leopoldville, in April, 1915. It was a small tree, with very large leaves, about 46 cm. long and 27 cm. wide, on short petioles (1 cm.). The young leaves, before complete expansion, are viscose, being covered with a resinous, sticky substance. The large, showy flowers are erect; their calyx ends in broad lobes; the corolla, about 26 cm. long, is dirty white in its upper part and greenish white in the tubular, lower portion. The egg-shaped fruit is 6 cm. long without the persistent calyx, 4 cm. thick, and deprived of ribs.

This species has no swellings on its branches and the stem is never hollow nor inhabited by ants. At the base of the leaf-blade (Fig. 94), on both sides of the midrib, there is an evagination of variable size, convex on the upper surface of the leaf, broadly open below. On some blades it consists of a mere inflation of the leaf-base, whereas in others it may be 4 to 6 mm. deep and pouch-like, 5 to 8 mm. long and 6 to 7 mm. broad. In all cases, however, on looking into it from the under side, one finds in the bottom, close to the midrib, a conspicuous pale brown gland which secretes a sweet substance. On some of the leaves of the specimen I examined near Leopoldville, a number of ants, *Crematogaster africana* subspecies *laurenti* variety *zeta* (Forel), had taken possession of these distended nectaria, closing the opening on the under side with a tent of fine, agglutinated, dark brown vegetable fibres. Frequently they were accompanied by coccids. Never having seen queens or brood of the ants in the leaf swellings, I can not regard these structures as forming part of the nest. Ants of the same variety occasionally build fibrous shelters over coccids which are fixed on the fruits of this *Randia*.

From the foregoing it is evident that *Randia physophylla* is not a true myrmecophyte in the sense generally meant by this term. Yet its relations with ants are not without interest, for here we have a primitive stage leading to the production of true ant-pouches such as those of *Scaphopetalum Thonneri*, *Cola Laurentii*, and certain South American Melastomaceæ.



Fig. 91. *Randia physophylla* K. Schumann: a, base of leaf-blade with the two swellings, seen from above, natural size; b, cross section of this base, one and one-half natural size; the nectarium is placed in n. Drawn from life at Leopoldville, April, 1915.

PLECTRONIA Linnæus

Plectronia LINNÆUS, 1767, 'Mantissa Plant.,' I, p. 52. K. SCHUMANN, in Engler and Prantl, 1891, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 91.

Canthium LAMARCK, 1783, 'Encyclop. Method.,' I, p. 602. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 132.

Shrubs or trees, often climbing or clambering bushes, occasionally spinous, with opposite leaves and branches, and acuminate stipules from a broad, often sheath-like base. Frequently some of the branches are sarmentose, hooked or winding; or the plant emits whip-like shoots, often many meters long, somewhat compressed, leafless or with small leaves, furnished with heavy, more or less recurved spines; these shoots trail along the ground or work their way up the trees. Flowers small, axillary, in dense cymes or umbels, or short panicles or clusters. Calyx-tube short, turbinate, campanulate, or hemispherical; limb short, 4- or 5-toothed or cleft, or subtruncate, deciduous. Corolla coriaceous; tube rather short, exceeding the calyx, glabrous outside, hairy with a ring of deflexed pilose hairs or rarely glabrous inside; throat rather constricted or dilated, often bearded; lobes 4 or 5, rarely 6, ovate or lanceolate, reflexed, usually glabrous, valvate in the bud (toward the apex sometimes induplicate-valvate). Stamens 4 or 5, rarely 6, exserted, inserted at the mouth of the corolla; filaments short; anthers ovate, or oval, or lanceolate, acute or obtuse, usually subsagittate at the base, as a rule glabrous, fixed at the back. Ovary 2-celled, fleshy. Style flexuous, filiform or thickened, exserted or equalling the corolla, usually glabrous. Stigma capitate, calyptriform or mitre-shaped, sometimes bifid at the tip, often sulcate. Ovules solitary, pendulous, orthotropous, the micropyle directed upward. Fruit a drupe, didymous, subdimidiate, or globose, 2-celled or by abortion 1-celled; stones 2 or 1, sometimes subrugose. Seeds pendulous, solitary, nearly straight or curved, sometimes bent into the form of a horseshoe round the placenta; testa membranous; albumen fleshy, sometimes ruminated; embryo cylindrical, nearly straight or curved, axile; cotyledons short, radicle superior.

Plectronia is a close relative of *Vangueria* Jussieu, but the latter has a three- to five-celled ovary and a drupe containing three to five one-seeded stones or consisting of one three- to five-celled stone. Many species of the genus *Psychotria* Linnæus, too, assume appearance and manner of growth of certain *Plectronia*, but differ in the ovule being erect, anatropous, with the micropyle opening downward, and in the inferior radicle of the embryo; on this account *Psychotria* is placed in a different tribe of the Rubiaceæ.

Plectronia is one of the largest genera of its family, some 200 species having been described from the tropical and subtropical parts of the Old World. About 150 species are known from Africa and of these twenty-four have been recorded from the Belgian Congo. Though only three of the African species have so far been mentioned as associated with ants, I suspect, from my observations in the Congo, that many others will turn out to be myrmecophytes.

***Plectronia connata* De Wildeman and Durand**

Plectronia connata E. DE WILDEMAN AND TH. DURAND, 1899, Bull. Soc. Bot. Belgique, XXXVIII, 2, p. 201; 1901, 'Reliquiæ Dewevreanæ,' p. 122. É. DE WILDEMAN, 1934, 'Études Flore Bas-et Moyen-Congo,' I, pt. 2, p. 204; 1912, *ibid.*, III, pt. 3, p. 488. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 161-162.

"Tree or shrub. Branches more or less terete, glabrous, inerm. Leaves opposite; petiolate, the petiole 1 to 1.5 cm. long; ovate-elliptic; dark green and sparsely pilose especially on the veins on the upper side, on the under side brown and paler in dried condition, sparsely pilose especially on the veins; the blade more or less decurrent along the petiole; abruptly and short acuminate at the apex, the acumen about 5 mm. long; rounded at the base; 7.5 to 10 cm. long and 4 to 5 cm. broad; on each side with about 7 lateral veins, which anastomose in curves before the margin and are united with the smaller veins. Stipules soon deciduous. Inflorescences axillary, 3 to 4 cm. long and about 3.5 cm. broad, opposite, dichotomous, bracteate at the base of the dichotomies; the bracts more or less broadly connate at the base, ovate-acute, 3 to 4 mm. long. Flowers pedicellate, the pedicel about 3 mm. long. Calyx campanulate, 5-toothed, the teeth short. Corolla 5-lobed; the tube 2.5 mm. long and about the middle 1.5 mm. broad; the lobes reflexed, about 2 mm. long and 1 mm. broad, ovate-acute. Stamens 5, not exerted; the filaments short. Style filiform, exerted over a long distance, about 1 cm. long, glabrous; the stigma capitate, short lobulate at the apex, about 0.5 mm. thick" (De Wildeman and Durand, 1899).

Belgian Congo: Lower Congo: Sefé River (Butaye). Middle and Upper Congo: Bolengi (M. Laurent); Likimi (Malehair); Lomami River, type locality (Dewèvre).

This species is easily recognized by the united bracts which form a sheath at the base of the ramifications in the flower panicles. According to Marcel Laurent, the natives at Bolengi call this plant "Boka na pombo" which means "ant-village." It is possibly one of the myrmecophilous members of the genus, and has therefore been included here.

Plectronia glabriflora (Hiern)

Plectronia glabriflora (HIERN) K. SCHUMANN, 1895, in Engler, 'Pflanzenwelt Ostafrikas,' C, p. 386. H. KRAUSE, 1911, 'Wiss. Ergebn. Deutsch. Zentr. Afr. Exp. (1907-1908),' II, p. 326.

Canthium glabriflorum HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 110; 1898, 'Catalogue Afr. Plants Welwitsch,' II, p. 474. K. SCHUMANN, 1891, Ber. Deutsch. Bot. Ges., IX, pp. 61-62. H. KOHL, 1909, Natur u. Offenbarung, LV, p. 162.

Canthium polycarpum SCHWEINFURTH Mss., 1877, ex Hiern, in Oliver, 'Flora of Tropical Africa,' III, p. 139.

"An unarmed tree, 40 to 50 feet high, with palm-like habitus; branches erect-patent, obtusely angular, glabrous or somewhat hispid. Leaves oval, shortly and abruptly acuminate, with a broad somewhat excavated base, thinly coriaceous, scabrous-hispid or glabrate above, turning reddish when dry, more or less hispid on the veins beneath, 3 to 5 by $1\frac{1}{2}$ to $2\frac{1}{2}$ in.; lateral veins about 7 to 8 pairs; petiole $\frac{1}{2}$ to $\frac{3}{8}$ in., hispid or glabrate; stipules ovate, $\frac{1}{8}$ to $\frac{1}{6}$ in. long. Flowers $\frac{1}{8}$ in. long (exclusive of the style), on short puberulous or glabrate pedicels, many together, in dense dichotomous globose panicles of 1 to $1\frac{1}{2}$ in. diameter; common peduncle glabrate or puberulous, short or ranging up to $\frac{1}{2}$ in., spreading, sometimes unilateral. Calyx-tube glabrous; limb truncate or obscurely toothed, glabrous or ciliate. Corolla glabrous outside, bearded inside; lobes 5, subobtusate. Disk glabrous. Stigma elongate-calyptiform, much exserted" (Hiern, 1877).

San Thomé: at 1000 feet (Mann; Welwitsch).

Southern Nigeria: Old Calabar (W. C. Thomson).

Cameroon: Barombi (Preuss).

Belgian Congo: Kwidjwi Island near Mgaturu in the forest (Mildbraed). North-eastern Region: Nabambisso River in the Niam-Niam Country (Schweinfurth).

Angola: Malange (Buchner).

Preuss, who observed this species in Cameroon, calls it an "ant-plant." According to Schumann (1891), the ants live inside the hollow stem and probably also in the horizontal branches. No other observations have been made on this form and its description is reproduced here chiefly on account of its possible identity with *P. Laurentii*.

Plectronia Laurentii De Wildeman

Plectronia Laurentii É. DE WILDEMAN, 1906, 'Mission Emile Laurent,' III, pp. 294-296, Pls. xcvi-xcix; 1907, 'Études Flore Bas- et Moyen-Congo,' II, pt. 2, p. 174; 1908, *ibid.*, II, pt. 3, p. 348; 1910, *ibid.*, III, pt. 2, p. 294. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 268. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 160-161.

"Shrub reaching a height of about 2.25 m., with quadrangular stems showing opposite the leaves a groove pierced with openings which allow ants to enter the internodal cavity. Branches spreading, glabrous when full-grown. Leaves opposite, petiolate; the petiole reaching a length of 2 to 3 cm., ciliate on the sides; the blade wedge-shaped, rounded or almost subcordate at the base, very broadly cuneate or acuminate at the apex, more or less coriaceous, 7 to 28 cm. long and 6 to 16 cm. broad,

with 8 to 12 lateral veins on each side of the midrib. Leaf-blade with scattered hairs, appressed on the upper side, somewhat more abundant on the under side, especially on the veins, which are villose, scabrous, and ciliate on the margins. Stipules triangular, subapiculate, about 1 cm. long. Inflorescences axillary, opposite, reaching a length of 5 to 6 cm. and about equally broad. Common peduncle short, glabrous, 3 to 8 mm. long, with dichotomous ramifications which bear below each bifurcation a more or less regular ring of bracteoles. Flowers fasciculate at the end of the ramifications; the pedicel short, slender, accrescent on the fruit and sometimes reaching a length of 5 mm. Calyx with feebly widened limb, superficially denticulate, glabrous. Corolla about 2 mm. long, glabrous externally, with 5 lobes. Style unknown in adult condition. Fruit flattened, subreniform, 6 mm. high, 9 mm. broad, and 4 mm. thick, sometimes one-celled by abortion" (De Wildeman, 1906).

Belgian Congo: Middle and Upper Congo: Bokala; Irebu; Chumbiri; Bolengi; Fala (M. Laurent); Lukolela (Pynaert); Bolombo; Nouvelle-Anvers; Malema (E. and M. Laurent). Eastern Congo Forest: Romee (H. Kohl); Tshopo River near Stanleyville (March 6, 1915; J. Bequaert; Coll. No. 7042); between Walikale and Lubutu (village of Pale, January 12, 1915; J. Bequaert; Coll. No. 6585); Paku (Seret).

It would seem from the description that *Plectronia glabriflora* (Hieru) is rather closely allied to, if not identical with, *P. Laurentii*; it is hardly to be expected that a plant so commonly found throughout the Congo Basin is absent from Cameroon and Angola.

ECOLOGY OF *Plectronia Laurentii*

The following notes were made on specimens in the forest region between Walikale and Lubutu (near the village of Pale, January, 1915; Coll. No. 6585) and along the Tshopo River near Stanleyville (March, 1915; Coll. No. 7042). This plant is a bush or small tree, about 4 to 7 meters high, with an erect, straight trunk, bearing from a short distance above the ground regularly opposite, nearly horizontal branches. The most striking feature is the squareness of the limbs which, on the younger parts of the plant, show four very pronounced longitudinal grooves interrupted at the nodes only. Above the nodes, where the myrmecodomatia are located, the depressions expand into four broad, flat sides, the stem being almost regularly square on a cross-section. Older branches often become more cylindrical, only slight traces of the longitudinal furrows being left. The leaves are short petiolate, large and broad, as much as 28 cm. long and 16 cm. wide. The stipules drop off early. While the stalk and limbs are glabrous and smooth, the leaves are slightly hairy and somewhat rough.

Both the trunk and lateral branches of *P. Laurentii* were inhabited by ants, of the form *Crematogaster africana* subspecies *laurenti* (Forel) in the case of the specimens from the Tshopo River, and of the variety

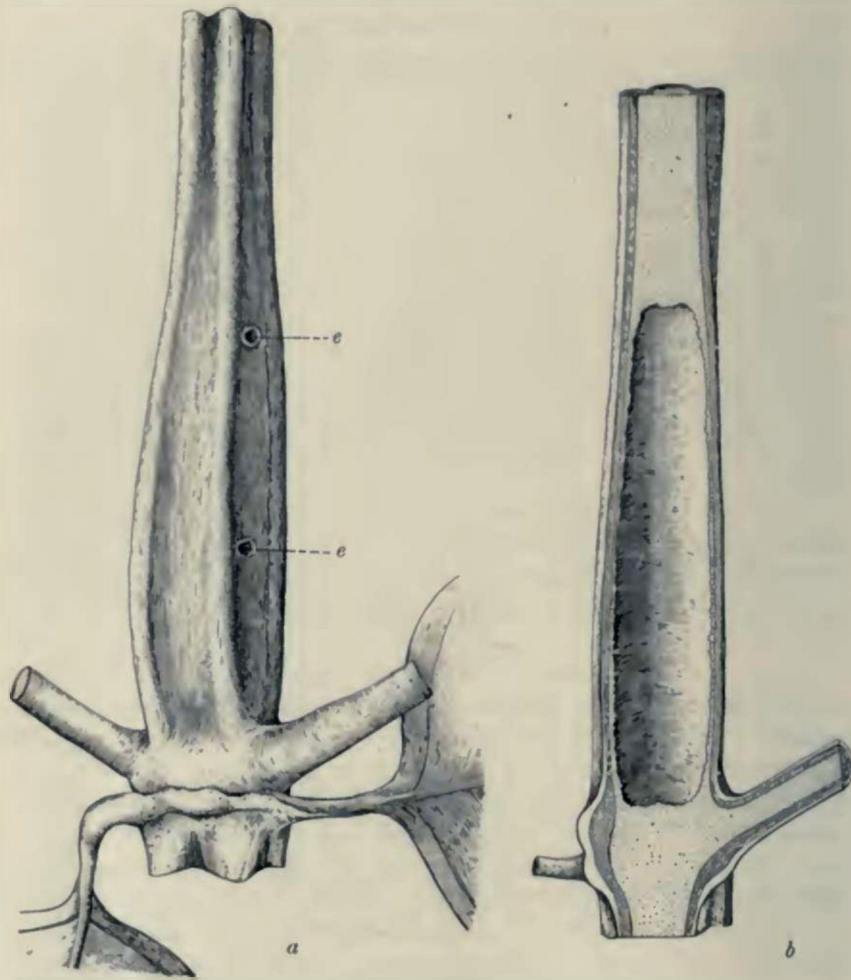


Fig. 95. *Plectronia Laurentii* De Wildeman: *a*, portion of branch with swelling above node inhabited by ants, showing apertures (*e*) to the domatium; *b*, longitudinal section of this myrmecodomatium. Drawn from life at Pale, between Walikale and Lubutu, January, 1915; natural size.

zeta (Forel) of that race in those found between Walikale and Lubutu. The older stalks of the plants are not much swollen, but the medullary cylinder is almost completely excavated, even the partitions at the nodes being occasionally perforated. In younger branches the various myrmecodomatia are more distinct; they are then moderately pronounced, quadrangular swellings, with the flat sides separated by slightly raised, obtuse ridges (Fig. 95*a* and *b*). They usually extend the basal two-thirds

of each internode and very gradually disappear in the upper part toward the node. The internal cavity is quite spacious, 6 to 7 cm. long and 10 to 15 mm. wide. An examination of very young shoots shows that the swellings are normal productions of the plant and that the cavities originate through the drying of the pith before the ants gnaw apertures. Hollows inhabited by these insects present a number of small, circular exit holes, which in my specimens were commonly located on any one of the sides. According to Kohl (1909, p. 161), they are placed on the surfaces facing the lower leaf pair, but this is far from being the rule. Many swellings, especially on the younger branches, have only one aperture; more commonly there are 2 to 4 entrances to each cavity, and in some cases as many as 12 to 15.

At least on the younger portions of the plant, every domatium contains a complete ant colony, with a queen, workers, and brood. Frequently coccids also are present and those found by Kohl near Stanleyville, together with *Crematogaster*, in the swellings of *P. Laurentii* have been described by Newstead (1910, p. 18) as *Hemilecanium recurvatum*. A number of such scale insects were also fixed on the outer surface of the stem, especially near the nodes, within tents of plant-fibres built by the ants and often communicating with their cavities. Kohl (1909, p. 161) further mentions that some of the internodes of a *Plectronia* in that locality were occupied by small, white caterpillars, while others were inhabited by ants.

Plectronia Laurentii was discovered at various places along the banks of the Middle and Upper Congo by Em. Laurent, who has given in his field-notes a good account of its relations with ants (De Wildeman, 1906, pp. 294-296). Much additional information on this species has been published by H. Kohl (1909, pp. 160-161). These observations agree in most details with mine.

The ants, all of the genus *Crematogaster*, found associated with *P. Laurentii* are evidently facultative inhabitants of these plants. The following forms have been recorded thus far:

Crematogaster africana (Mayr), variety. Belgian Congo; found by Em. Laurent (Kohl, 1909, p. 161).

C. africana subspecies *laurenti* (Forel). Found by Laurent at Bokala (Kohl, 1909, p. 160), by Kohl at Isangi and Stanleyville (Forel, 1909, p. 60), and by myself near the Tshopo River.

C. africana subspecies *laurenti* variety *zeta* (Forel). Between Walikale and Lubutu (J. Bequaert) and in the Congo (Kohl; see Forel, 1909, p. 70).

C. africana subspecies *winkleri* (Forel). Belgian Congo (Kohl; see Forel, 1909, p. 69).

C. africana subspecies *winkleri* variety *sickendeyi* (Forel). With regard to this variety Forel (1916, pp. 409-410) writes:

Kohl has collected various forms transitional between the race *winkleri* and the variety *sickendeyi*, on one occasion in a nest, probably usurped, of *Tetramorium aculeatum*, also in myrmecophilous plants or in termitaria. His No. 6S bears the following interesting remark: "Ant from plants. Lives in and on the myrmecophyte *Plectronia Laurenti* De Wildeman. Five meters above the ground the trunk bore a carton nest, 40 to 50 cm. high, of this ant. But it inhabits at the same time all the hollow branches of the plant. Makanga on the Okiavo River." One may conclude from this that there is no absolute contrast between the carton nest of *buchneri* and the habit of living in hollow stalks.

ECOLOGY OF UNIDENTIFIED AFRICAN SPECIES OF *Plectronia*

In addition to the species just studied, I have found caulinary swellings inhabited by ants on a number of rubiaceous plants which are provisionally regarded as belonging to the genus *Plectronia*. It is possible, however, that one or more may be species of related genera, such as *Vangueria*, *Grumilea*, or *Psychotria*. At any rate, I have been unable to identify them with any of the described African Rubiaceæ and they may even represent forms new to science. Their correct identification will undoubtedly be made later when the study of my herbarium, now in the hands of Mr. De Wildeman, Director of the Brussels Botanic Garden, is more advanced.

Plectronia species A.—This species was first observed on the forested banks of the Aruwimi River near the village of Bafwalipa, between Bomili and Avakubi (December 29, 1913; Coll. No. 1696). It also occurred in the Ituri Forest, near the village of Tete, between Penge and Irumu (February 22, 1914; Coll. No. 2567), and, in company with Mr. Lang, I came across it again along the Tshopo River near Stanleyville (March 6, 1915; Coll. No. 7043). It is a climbing, much-branched bush of the forest, with simple, opposite, short petiolate or subsessile leaves, which are asymmetric and cordate at the base. There were no thorns or spines on the specimens I examined. The entire plant—leaves and stems—is abundantly covered with long, erect, brownish hairs. The flowers are small and clustered in corymbs in the axils of the leaves.

Myrmecodomatia (Fig. 96) are found on some of the branches only. They consist of spindle-shaped swellings on the lower third of an internode, are about 30 mm. long and 8 mm. thick, and placed immediately above the node. The domatium is a spacious, rather thin-walled cavity. When inhabited, it is almost wholly cleaned of medullary tissue and com-

municates with the outside by means of a broad, irregular aperture, placed about the middle of the swelling. It was noticeable that leaves at the base of the expanded area are shorter and more heart-shaped than elsewhere on the plant. In this case, too, the enlargements are normal productions and their inner cavity originates through the drying of the pith and without the agency of ants.

Mr. Lang collected specimens of *Cataulacus tragaordhi* variety *plectronix* Wheeler in domatia of this species along the Tshopo River, while I found a few workers of *Engramma kohli* Forel in other swellings of the same plant.

Plectronia species B.—I obtained this *Plectronia* in the Rain Forest near Avakubi (January 10, 1914; Coll. No. 1871) and Penge (February 14, 1914; Coll. No. 2478), in both cases on the banks of the Ituri River. It is a creeper whose main stem, about 20 mm. thick near the ground, hangs freely in true liana-fashion between the bushes, while the branched upper part spreads its leaves over the crowns of low trees and undergrowth. Evidently closely related to the preceding form (species A), it differs chiefly in being more sparsely hairy, and in having myrmecodomatia of another shape. Furthermore, the main stalk bears at the nodes strong thorns placed in pairs and formed by the hardened bases of aborted branches.

In this species ants inhabit the thickened main stem, as well as the branches. On the latter the myrmecodomatia (Fig. 97a) are elongate, spindle-shaped swellings of the nodal region, extending about as far below as above the node. They are almost completely excavated and rather thin-walled; their internal cavity is 9 to 11 cm. long, 8 to 10 mm. wide, and even extends a short distance into the slightly swollen bases of the opposite branches. In this case too the expansions are normally present on the plant and their medullary tissue soon dries up, the ants merely piercing the orifices and removing the remains of pith. When occupied by these insects, the domatia usually have a number of apertures, placed above the node in an irregular, longitudinal row; there is often an exit hole also at the enlarged base of the side twigs. Even the nodes of the main stalk (Fig. 96b) are tenanted but, owing to the thickening of

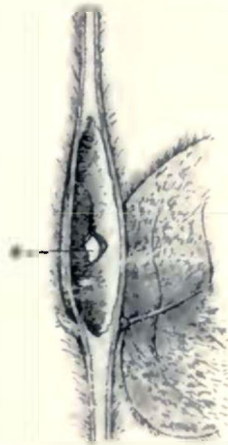


Fig. 96. *Plectronia* species A. Portion of branch in longitudinal section, showing a domatium occupied by ants: c, aperture leading into the cavity. Drawn from life at Bafwalipa, between Bomili and Avakubi, December, 1913; natural size.

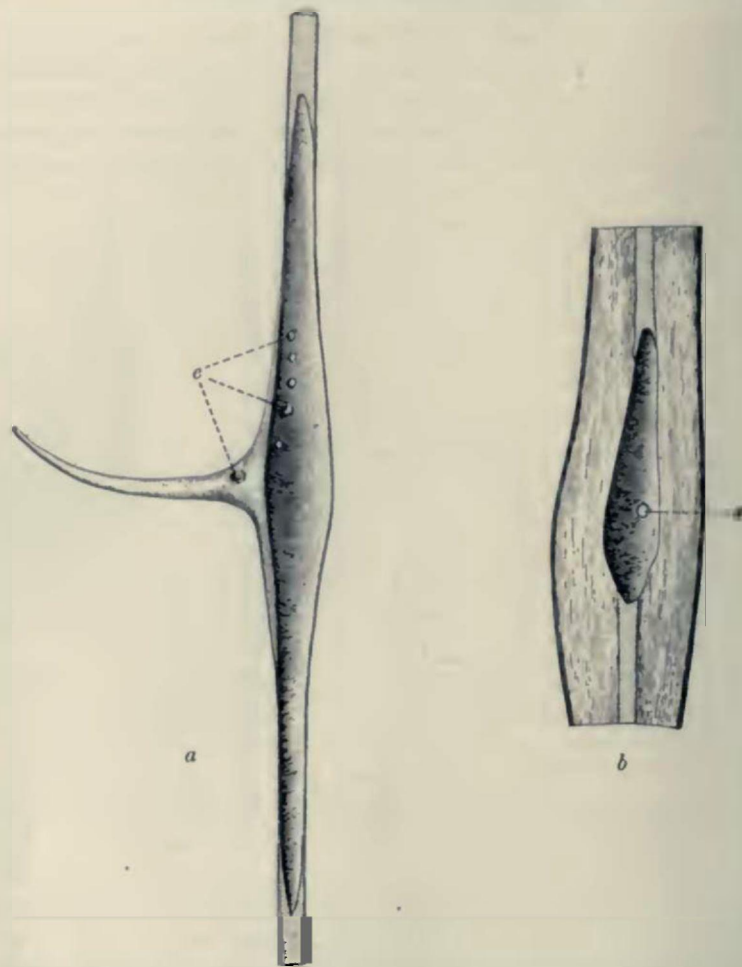


Fig. 97. *Plectronia* species B; a, portion of younger branch in longitudinal section, showing myrmecodomatium at the node which also extends into the base of the lateral ramification; b, portion of main stalk, showing shape of domatium in older parts of plant; c, apertures leading into the cavity. Drawn from life at Avakubi, January, 1914; natural size.

the woody cylinder, are but slightly or not at all swollen and their inner cavity is much reduced (3 to 4 cm. long, 5 to 7 mm. wide); they usually present two openings placed on a crateriform elevation, one above each of the nodal thorns. Frequently there are scars of other perforations which have been closed by callus growth.

The ants found inside this *Plectronia* belonged in both localities to a small, unidentified species of *Crematogaster* which can hardly give pro-

tection to its host. Even though most of the domatia were inhabited, the leaves had been eaten by caterpillars and both young branches and leaves bore numerous insect galls—elongate, pear-shaped swellings ending in a recurved tail-like apex and on one side of the tail with a small exit hole leading into a central chamber; their outer surface covered with many erect, brownish-red hairs; all the galls seen were empty.

Plectronia species C.—In the Semliki Forest, near Lesse (June 15, 1914; Coll. No. 4753), I came across a creeper whose many hanging branches had covered the bushes at the edge of a clearing. It is perhaps specifically identical with the preceding form (species B), possessing most of its general characters. Yet the domatia are sufficiently different in shape to deserve separate description.

The ant-swellings (Fig. 98) are short and broadly spindle-shaped, and occupy the lower part of the internodes of most of the branches. The inner cavity is very spacious, 6 to 8 cm. long and 15 to 20 mm. wide, continues a little below the node, and extends also into the slightly swollen bases of the side branches. A peculiarity of this *Plectronia* is that the domatia lack circular apertures, but communicate with the outside by means of two long slits, placed opposite each other in the upper part of the swelling, above each of the side branches. Often these openings are partly closed by callus growth. The plant at Lesse was inhabited by populous colonies of a small *Crematogaster* with a queen, numerous workers, and brood at various stages; also coccids which were fixed on the calus tissue near the inner margin of the slits.

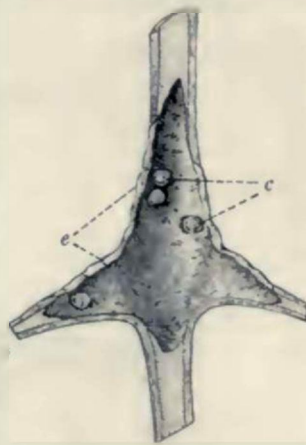


Fig. 98. *Plectronia* species C. Longitudinal section of swollen node inhabited by ants: e, callus growth bordering the slit which leads into the cavity; c, coccids attached to inner walls. Drawn from life at Lesse, June 1914; natural size.

CUVIERA de Candolle

Cuviera A. DE CANDOLLE, 1807, Ann. Mus. Paris, IX, p. 222; 1830, 'Prodromus Regn. Veget.,' IV, p. 468. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 150. K. SCHUMANN, 1891, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' IV, pt. 4, p. 91.

Glabrous shrubs or small trees, rarely with puberulent young branches. Leaves usually large, broadly ovate, entire, opposite, coriaceous or leathery; stipules apiculate, united into a short sheath between the bases of the petioles. Flowers polyga-

mous, with large foliaceous bracteoles, in many-flowered, axillary panicles. Sepals 3 to 5, almost free or shortly united at the base, foliaceous, spreading, often unequal, persistent, much longer than the petals. Corolla hypocrateriform, with a short, straight tube furnished inside with a ring of deflexed hairs, and large, fleshy lobes. Stamens 5, exserted, placed on the mouth of the corollar tube. Ovary 3- or 5-celled, each cell with one ovule. Ovule suspended, with upper micropyle and flattened funiculus. Style with a semiglobose, cap-shaped or mushroom-shaped, sulcate stigma. Fruit an obovate drupe, often oblique or falcate, distinctly ribbed, with 3 to 5 seeds.



Map 46. Distribution of *Cuviera*, a genus of myrmecophytic plants.

Cuviera is a strictly African genus, of which fourteen species have been described. Its general distribution is shown on Map 46. The genotype, *C. acutiflora* de Candolle, is found in Upper Guinea. Only one form, *C. australis* K. Schumann, has been described from South Africa. All the others occur within the limits of Engler's Western Forest Province, either in the Rain Forest proper or on the forested river banks of the adjoining Savannah, below 3000 feet. With the possible exception of *C. australis*, all the members of the genus may be myrmecophytes

and their descriptions have, therefore, been reproduced here. Some of these so-called species are perhaps mere synonyms.

***Cuviera acutiflora* de Candolle**

Cuviera acutiflora A. DE CANDOLLE, 1807, Ann. Mus. Paris, IX, p. 222; 1830, 'Prodromus Regn. Veget.', IV, p. 468. BENTHAM AND HOOKER, 1849, 'Niger Flora,' p. 407. HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 156.

Cuviera africana SPRENGEL, 1825, 'Syst. Veget.', I, p. 760.

"A glabrous shrub, 15 to 20 ft. high. Branches terete, divaricate, supra-axillary. Leaves oval-oblong, acuminate, subequal and rounded or somewhat narrowed at the base, coriaceous, glossy, rather or scarcely paler beneath, 4 to 10 by $1\frac{3}{4}$ to 4 in.; some 4 to 6 in. wide (Bentham); lateral veins about 6 to 10 pairs, not conspicuous; petiole $\frac{1}{3}$ to $\frac{1}{4}$ in.; stipules ovate, apiculate, $\frac{1}{2}$ in. long, connate and sheathing below, keeled, hairy within. Flowers greenish, $\frac{3}{8}$ to $\frac{2}{5}$ in. long in bud, on short, slender pedicels, very numerous, in ample, divaricately branched, rather lax, axillary and terminal, shortly pedunculate, dichotomous panicles of 2 to 6 in. diameter; bracteoles elliptic-linear, $\frac{3}{8}$ to 1 in. long, accrescent. Calyx green; segments to $\frac{1}{2}$ in. long, linear-oblong, spreading, persistent. Corolla green and orange; segments lanceolate, caudate-acute, $\frac{3}{8}$ in. long, spreading. Ovary 5-celled; style glabrous. Fruit obliquely egg-shaped, $\frac{3}{4}$ to $\frac{5}{8}$ in. long, obtusely 5-sided; pyrenes 5 or fewer" (Hiern, 1877).

Sierra Leone, type locality (Smeathman).

Ivory Coast: Grand Bassam (Th. Vogel).

Cameroon: Ambas Bay (Mann).

***Cuviera angolensis* Hiern**

Cuviera angolensis HIERN, 1898, 'Catalogue Afr. Plants Welwitsch,' II, p. 483. E.

DE WILDEMAN AND TH. DURAND, 1901, Bull. Herbar Boissier, (2) I, p. 826; 1901, 'Reliquiae Deweyreanae,' p. 124. E. DE WILDEMAN, 1901, 'Etudes Flore Bas- et Moyen-Congo,' I, p. 205; 1907, *ibid.*, II, pp. 78 and 173; 1908, *ibid.*, II, 3, p. 348; 1910, *ibid.*, III, 2, p. 295; 1912, *ibid.*, III, 3, p. 489; 1906, 'Mission Emile Laurent,' III, pp. 296-299, Pl. cvi. H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 163-166. TH. AND H. DURAND, 1909, 'Sylloge Flor. Congol.,' p. 271. (K. Schumann, in Engler and Prantl, 1891, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 94, fig. 33J, without description; also mentioned without description by K. Schumann, 1890, Verh. Bot. Ver. Brandenburg, XXXI, 2, p. 121, and 1891, Ber. Deutsch. Bot. Ges., IX, p. 56).

"A small glabrous pyramidal tree, 12 to 20 ft. high, or in cultivated fields (*arimos*) usually only 8 to 12 ft. Sap milky. Trunk slender, straight, destitute of branches below, but densely armed with opposite, decussate, strong, very acute, quite patent spines of 1 to 2 in. in length. Branches and branchlets green, the latter swelled at the nodes. Leaves long, opposite, usually cuspidate at the apex, oblique and rounded at the base, papery, smooth, 4 to 9 in. long by $1\frac{1}{2}$ to 4 in. broad, dull-green above, paler beneath, those on the older branches pendulous; petiole $\frac{1}{8}$ to $\frac{1}{2}$ in. long; lateral veins about 8 on each side of the midrib, rather slender and beneath conspicuous. Stipules sheathing, keeled, acuminate, about $\frac{2}{8}$ to $\frac{1}{2}$ in. long. Inflorescence axillary, branched, 2 to 4 in. long, pale yellow-greenish outside throughout except a bright rosy stellate patch about the naked throat of the corolla; pedicels very short;

common peduncle $\frac{1}{2}$ to 1 in. long; bracteoles sub-linear, ranging up to 1 in. in length. Calyx including and adnate to the ovary; tube short, campanulate-ventricose, obtusely 3- to 4-angular, deeply 3- to 5-lobed; the segments elongate-lanceolate, unequal in length, bract-like, exceeding the corolla, herbaceous-green, $\frac{1}{2}$ to 2 or 3 in. long. Corolla shortly salver-shaped, fleshy-coriaceous, deep herbaceous-green outside; tube short, bright-red inside, at the base inside with a ring of shiny silvery hairs directed downward; limb 5-cleft, shortly rotate; segments lanceolate or ovate-acuminate, rigid, green, expanded in a stellate manner in full flower, valvate at the base in estivation: the tips long, acuminate or subulate, contorted in the bud. Stamens 5, inserted in the sinuses of the corolla-lobes around the ring of hairs; rigid, exserted; filaments compressed-cylindrical, fleshy, curved-patent at the time of flowering; anthers ovate, cordate, introrse, 2-celled, obtuse at the apex, basifixed; cells separate at the base, cohering at the apex longitudinally, yellow. Ovary adnate to the calyx-tube, 5-celled; cells 1-ovuled; disk a little elevated, flat; style thick, columnar, rosy, densely pilose; stigma mitriform, large, obtuse, stigmatose and cleft at the apex. Fruit oblique, deeply furrowed, about 1 in. long, crowned with the more or less persistent calyx-limb or with its remains" (Hiern, 1898).

Angola: Golungo Alto: "among the mountainous forests of Alto Queta," type locality (Welwitsch).

Belgian Congo: Kisantu (Gillet). Kwango: Kikwit (Lesrauwaet). Middle and Upper Congo: Lukolola (Dewevre); Likimi (Malehair); on the left bank of the Congo below Bolombo; Malema; Lic (Em. Laurent); Irebu (Pynaert); Eala (M. Laurent). Northeastern Congo forest: Isangi; Tshopo River near Stanleyville (Em. Laurent); Romee (H. Kohl); Nala; Lifungula (Seret); Manyema (Berger).

Cuviera australis K. Schumann

Cuviera australis K. SCHUMANN, 1899, Engler's Bot. Jahrb., XXVIII, 1, p. 78.

"Shrubby, with rigid, divaricate, terete, glabrous branches; the young branches flattened and puberulent. Leaves with short petioles, oblong, ovate, or oblong-lanceolate, obtuse, rounded or acute at the base, glabrous above; on the under side softly puberulent on the primary veins, otherwise glabrescent; discolored, herbaceous. Stipules subulate or filiform from a broad base, not setose inside. Cyme twice, more rarely three times trichotomous, axillary, appearing below the leaves, pedunculate, minutely puberulent, with very slender branches. Flowers pentamerous, pedicellate. Ovary sub-semiglobose, slightly hairy, 5-celled. Calyx divided to near the base into foliaceous, subspatulate, elongate lobes. Corolla divided beyond its middle into five lobes, which are lengthened subtriangular and hirsute externally; tube glabrous on the outer side. Style exserted for twice the length of the tube, with 5-toothed stigma.

"The flowering branch at hand is 30 cm. long and 2 to 2.5 mm. thick at the base where it is covered with gray bark. The petiole is 3 to 6 cm. long and very finely pilose; the blade is 3 to 5 cm. long, 1.1 to 2.7 cm. broad in the middle, traversed on each side of the midrib by 5 or 6 stronger veins which are slightly prominent on both sides, black above, gray below. The stipules are 2 to 3 mm. long. The flowers are borne on finely pilose pedicels, 5 to 9 mm. long. The ovary is 2 mm. long, the calyx 7 to 8 mm.; its lobes are very obtuse and reach a width of 2 mm. above. The corolla-tube is 3 to 4 mm. long; its lobes are 6 to 7 mm. long and are very finely pilose outside. The anthers are a little over 1 mm. long and inserted on a filament of 0.5 mm. The style is exserted for 6 to 7 mm. out of the corollar tube.

"Different from all the other species, which occur in tropical West Africa only, by the much smaller flowers and leaves. I believe I should have distinguished two forms, one of the specimens is more hairy and has much smaller flowers. Schlechter thinks, however, that both specimens come from one and the same bush" (K. Schumann, 1899).

Portuguese East Africa: Delagoa Bay, at 30 m. (Schlechter).

Cuviera calycosa Wernham

Cuviera calycosa WERNHAM, 1914, Journ. of Botany, London, LII, p. 7.

"Tree 90 feet high, glabrous, nigrescent in dried condition, with terete branches later on covered with grayish bark. Leaves parchment-like, elliptic or oblong, small for the genus, shortly and narrowly acuminate, obtuse, acute at the base, glabrous; petiole very short. Stipules small, lanceolate, acuminate, caducous except for the broad base. Inflorescences having few flowers, dichotomous, rather loose; bracts oblong-lanceolate, obtuse. Calyx large, much exceeding the corolla; with uneven, ovate-lanceolate, acuminate and very acute lobes. Corolla with a broadly funnel-shaped to cylindrical, rather short tube; its 5 lobes acuminate with long appendages and a few scattered, rather long hairs. Drupe very glabrous, crowned by the persistent limb of the calyx.

"A remarkable species, the nearest affinity being clearly *C. nigrescens* (Scott-Elliott); the present species is distinct, especially in the very large calyx and small corolla. The leaves measure 10 to 11 cm. \times 4 to 4.5 cm., with petiole about 1 cm. long; secondary veins 5 to 6 pairs; stipules 6 to 8 cm. long. Peduncle 3 cm.; cyme 11 to 12 cm. wide, 5 to 6 cm. long. Pedicel 5 mm.; calyx-tube minute, lobes 3 to 3.5 cm. \times 4 to 7 mm. Corolla-tube barely 5 mm. long, and nearly as much in average breadth; lobes, flat part 4 to 5 mm., setae over twice that length. Berry 1.4 cm. \times 1.1 cm." (Wernham, 1914).

"Youngest flowers white, older ones cream, oldest thin orange. Centre of flower greenish. Calyx-lobes bright green, with margin and setae white. Setae of corolla-lobes white; anthers dark-purplish brown; style white, stigma pale green" (Mrs. Talbot).

Southern Nigeria: near Esuk Ekkpo Abassi in the Eket District (Mr. and Mrs. P. A. Talbot).

Cuviera latior Wernham

Cuviera latior WERNHAM, 1918, Journ. of Botany, London, LVI, p. 311.

"A very glabrous shrub, with very smooth, subterete, moderately robust, striate branches, swollen and excavated at the nodes (apparently with a myrmecodomatium). Leaves large, parchment-like, broad, oblong, but little acuminate, cordate and very unevenly oblique at the base; petiole short, though distinct; primary veins conspicuous, 10 to 12 on each side. Stipules connate into a broad sheath, which is very short, arcuate above, and obscurely spiculate between the petioles. Flowers large for the genus, placed in loose, few-flowered, forked cymes; common peduncle much flattened; pedicels very short. Calyx with 3 lobes which are full of veins, broadly lanceolate, long acuminate, large and leaf-like. Tube of the corolla broad and very short, its 5 lobes oblong, very acuminate, subsetaceous and cucullate at the apex. Ovary deeply sulcate; style thick, densely and finely hispid.

"Notable for the broad calyx-lobes and the large flowers. Leaves 20 to 26 cm. \times 8 to 9 cm., with petiole 6 to 8 mm. at longest; stipule-sheath 2.5 mm. deep. Peduncle 2 cm. long, forking at the tip into two floriferous branches about 10 cm. long. Calyx-lobes 3 to 3.5 cm. long, and 1 cm. or more broad. Corolla-tube barely 4 mm. long; lobes 1.6 cm. \times 4 mm. Anthers 2 mm. long. Style 1 cm. long" (Wernham, 1918).

Belgian Congo: north of Boyeka (Nannan).

Cuviera Ledermannii Krause

Cuviera Ledermannii KRAUSE, 1912, Engler's Bot. Jahrb., XLVIII, p. 418.

"Erect shrub or small tree, with slender, strong, glabrous branches and branchlets, which are swollen, a little flattened and hollow at the nodes; bark smooth, dark brown or almost black in spots. Leaves large, short-petiolate; stipules broadly ovate, minutely acuminate at the apex, soon dropping, connate at their base into a short sheath which persists longer; petiole short, strong, grooved above to near its base; blade thick, coriaceous, very glabrous on both sides, oblong or elliptic-oblong, rather long acuminate at the apex, obtuse at the base or even shortly decurrent along the petiole; primary veins 9 to 12, slightly prominent above, more distinctly so below, running in an obtuse angle from the costa. Inflorescence axillary, short, with few flowers; bracts large, narrowly oblong, obtuse. Ovary semiglobose; lobes of the calyx large, narrowly oblong, acute, 2 to 3 times longer than the ovary; tube of the corolla cylindrical, scarcely broadened above, the lobes lanceolate-oblong, acute, as long as or longer than the tube; stamens with very short filaments, the anthers small, oval-oblong; style rather highly exserted above the tube of the corolla, crowned with a rather large, mitriform stigma.

"The plant is a shrub or small tree; the branches which I have before me are covered with dark brown or almost black bark; they are 2 to 3 dm. long and 5 mm. thick at their base; the thickened, hollow swellings, above the nodes, are 7 to 9 mm. in diameter; they undoubtedly are inhabited by ants. The stipules are 8 to 10 mm. long, the petioles 1.2 to 1.6 cm. The blades in a dried state are brownish-green to gray-green and, including their apex of 1.2 to 1.6 cm., are 1.8 to 2.5 dm. long, 7 to 11 cm. broad. The inflorescences attain a length of 7 cm. The large bracts, which may reach a length of 1.8 cm., in drying take on a leather-brown color, as do also the sepals. The ovary has a diameter of 2.5 mm. The sepals are 7 to 8 mm. long. The corolla, white in life, turns dark brown in drying; its tube is 4 to 5 mm. long, its lobes 5 to 6 mm. The filaments are about 0.8 mm. long, the anthers 1.2 mm. The style, including a stigma of about 1.5 mm., measures 8 mm." (Krause, 1912).

Cameroon: near Nkolebunde on the Nanga-slopes in a rather sparsely wooded place, at about 200 m.; also near Malende in the vicinity of Nkolebunde in dense, high forest with little underwood, at 150 m. (Ledermann; in flower during October).

The species agrees in most respects with *C. physinodes* K. Schumann, from which it is said to differ in "the branches, which are less strongly flattened and broadened at the nodes, and also in the darker, partly almost black bark."

Cuviera leniochlamys K. Schumann

Cuviera leniochlamys K. SCHUMANN, 1899, Engler's Bot. Jahrb., XXVIII, 1, p. 79.

"Shrub with slender, terete flowering branches, the flattened younger ones also glabrous. Leaves with a short petiole, oblong, shortly and very sharply acuminate, acute at the base, herbaceous, glabrous on both sides. Stipules glabrous, subulate from an oval base. Flowers fasciculate in small numbers in the axils of the leaves, shortly pedunculate. Ovary subglobose, glabrous. Calyx very large, divided to beyond the middle into 5 acute lobes, membranaceous. Corolla twice as long as the calyx, divided beyond its upper third into apiculate, narrowly lanceolate lobes, with a hairy ring above its base. Anthers comparatively small. Style pilose at the thickened base; stigma cap-shaped, 5-toothed.

"A bush 4 to 5 m. high, whose flowering branches of 12 to 15 cm. are scarcely 2 mm. thick at the base, and are covered with a gray to blackish epiderm. The petiole is 2 to 6 cm. long and slightly canaliculate above; the blade is 9.5 to 17 cm. long and 4 to 7 cm. broad, green when dry, traversed on each side of the midrib by 6 stronger veins, which are a little more prominent below. The stipules are hardly 5 mm. long. The ovary, black when dry, is 1.5 to 2 mm. long and up to 3 mm. thick. The white calyx is 13 to 15 mm. long and membranaceous. The ochre-yellow corolla is 3 cm. long, of which 2 cm. is the tube; a ring of white hairs hangs down, 3 to 4 mm. above the base inside. The stamens are included and scarcely 3 mm. long. The style is white-hairy at the base and 2 to 2.1 cm. long, with a stigma 3 mm. high.

"The species can not be confused on account of its large, cupuliform, white colored calyx and the style which is hairy at the base" (K. Schumann, 1899).

Cameroon: Bipindi (Zenker).

Cuviera longiflora Hiern

Cuviera longiflora HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 157. K. SCHUMANN, 1891, Ber. Deutsch. Bot. Ges., IX, p. 56; 1891, in Engler und Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 12, fig. 5. H. KONL, 1909, Natur u. Offenbarung, LV, p. 166.

"A glossy shrub of 25 feet or a small tree of 20 to 25 feet, glabrous or nearly so. Branches subterete, smooth. Leaves oval-oblong, cuspidate, oblique and hollowed at the base, spreading, thinly coriaceous, paler beneath, 6 to 12 by 2 to 4 in.; lateral veins about 10 to 12 pairs, inconspicuous; petiole $\frac{1}{3}$ to $\frac{3}{8}$ in.; stipules deltoid, keeled at the apex, hairy inside, $\frac{1}{4}$ in. long. Flowers $1\frac{3}{4}$ in. in diameter when expanded, on short pedicels, several together, in axillary panicles of 2 to 3 in. diameter; bracteoles narrowly elliptical, $\frac{7}{8}$ to $1\frac{1}{2}$ in. long; peduncle about 1 in. Calyx-segments lanceolate, $\frac{1}{2}$ to $\frac{3}{4}$ in. long. Corolla-segments $\frac{3}{4}$ in. long, lanceolate, acute. Anthers drooping. Ovary 5-celled; style pilose-hirsute below; stigma cernuous" (Hiern, 1877).

Cameroon: Mt. Cameroon, at 2000 to 3000 ft., type locality (Mann). Also found in Cameroon by Preuss.

The presence of myrmecodomatia is not mentioned in the original diagnosis of this species, but Schumann found conical swellings on the basal part of the internodes of specimens collected by Preuss in Cameroon. Two longitudinal rows of three or four superposed orifices, often surrounded by a thickened ring, led into a cavity containing small, black ants of the genus *Crematogaster*.

C. longiflora is so closely related to *C. angolensis* that the differences are not clear from the descriptions. Some of the plants which I observed in the Belgian Congo agreed equally well with the descriptions of each and it seems possible that future investigation will result in the synonymizing of *C. angolensis* with the earlier described *C. longiflora*. H. Kohl (1909, p. 166) states that *C. longiflora* differs specifically from *C. physinodes* and *C. angolensis* "in the sparse, short pilosity of the style, which is very strikingly narrowed toward the apex." The style of *C. physinodes* is described as glabrous, which is also the case with *C. acutiflora* and *C. subuliflora*. *C. angolensis*, however, agrees with *C. longiflora* in having the style pilose, as was mentioned in the original description and as I have observed in my Congo specimens.

***Cuviera macroua* K. Schumann**

Cuviera macroua K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, p. 352.

"Branches slender, not fistulose nor swollen, cylindrical, even the young ones flattened and glabrous. Leaves short petiolate, lanceolate or suboblong-lanceolate, subacuminate, acute at the base, margined, glabrous on both sides, somehow folded by drying. Stipules tubulose-connate, bidentate, accrescent, finally pierced by the inflorescences and withering away, villose inside. Flower panicle tripartite from the base, with many or dense flowers, glabrous. Bracts linear, acuminate. Ovary 5-celled. Sepals linear, acuminate, glabrous, united at the base into a cupule. Lobes of the corolla with very long appendages. Style hirsute.

"The flowering branches are 30 cm. long and only 3 mm. thick at the base; they are covered with brownish-black bark. The petiole is 3 to 5 mm. long and flattened above; the blade has a length of 9 to 15 cm. and in the middle is 2.5 to 4 cm. wide; it is crossed on each side of the midrib by 6 to 7 stronger veins which are prominent on both surfaces, but almost more so on the upper side; in dried condition it is black green above, leather-yellow below. The stipules are 7 mm. long. The 3 bracteoles are about 1.5 cm. long. The calyx has a total length of 1.6 cm., of which 1.3 cm. is to be allowed for the lobes. The corolla is 2 cm. long, half of this belonging to the appendages of the lobes. The stamens and anthers measure 1.5 mm.

"The species strikingly differs from all the West African ones in its small leaves and the long appendages of the corollar lobes" (K. Schumann, 1903).

Southern Nigeria: Lagos (Millen).

***Cuviera minor* Wright**

Cuviera minor C. H. WRIGHT, 1906, Bull. Misc. Inform. Bot. Gard. Kew, p. 105.

"Differs from the other species in its smaller, membranous leaves.

"A small tree. Branches ash-colored. Leaves ovate or oblong-ovate, acuminate, slightly uneven-sided, rounded or short cuneate at the base, glabrous; with about 6 lateral veins on each side of the midrib; 11.5 cm. long, 4.5 cm. broad. Petiole grooved above, slender. Stipules broadly triangular, dropping. Inflorescences axillary, with many flowers, 4 cm. long. Bracts oblong, narrowed at the base and at the apex, 8 mm. long. Lobes of the calyx 5, subfoliaceous, lanceolate, 8 mm. long. Tube of the

corolla 4 mm. long, inside near the base with a ring of hairs bent downward. Lobes of the corolla triangular, acuminate-caudate, 1 cm. long, pilose externally, yellowish. Stamens 5, inserted between the lobes of the corolla; anthers sagittate, twice as long as the filaments. Ovary 5-celled, each with one ovule. Style 8 mm. long; stigma flask-shaped" (C. H. Wright, 1906).

Gold Coast: Kimaha (Johnson).

***Cuviera nigrescens* (Scott-Elliot)**

Cuviera nigrescens (Scott-Elliot) WERNHAM, 1911, Journ. of Botany, London, XLIX, p. 321.

Vangueria nigrescens SCOTT-ELLIOT, 1894, Journ. Linn. Soc. London, Botany, XXX, No. 206, p. 81. OLIVER, 1894, in Hooker's 'Icones Plantarum,' XXIII, pt. 4, Pl. MMCCCLXXXIII.

Cuviera trichostephana K. SCHUMANN, 1897, Engler's Bot. Jahrb., XXIII, 4, p. 461.

"A shrub with terete, grayish, glaucous branches, in youth black and covered with lenticels. Leaves becoming black by drying, very glabrous (except in the axils of the veins where they are hirsute), oblong-ovate or obovate, obtusely acuminate, subcuspidate, with coriaceous margin, narrowed at the base; 5 to 8 cm. long and 2 to 3 cm. broad; 5 or 6 pairs of lateral veins; petiole 6 to 8 mm. long. Stipules hirsute inside, rounded at the base, elongate-acuminate along the back, 3 to 5 mm. long. Peduncles faintly pilose, 5- to 10-flowered, 8 mm. long. Pedicels about 6 mm. long. Bracts ovate, obtuse, with reticulate venation, 8 to 9 mm. long and 4 mm. broad. Calyx with 5 large lobes, which are lanceolate, subacute, 8 to 9 mm. long and 2 mm. broad. Lobes of the corolla caudate-acuminate, 15 to 17 mm. long (the acumen 3 to 4 mm.), sparsely hirsute on the outside with white hairs 1 mm. long, internally with a ring of reflexed pile. Filaments 2 mm., anthers 1 to 2 mm. long. Stigma cylindrical, large, 1 to 2 mm. long and 1 mm. broad. Ovary 5-celled" (Scott-Elliot, 1894).

Sierra Leone: in the forest between 1000 and 3600 feet; near Kafogo in Limba and near Falaba (C. F. Scott-Elliot).

Liberia: Golah Forest (Bunting).

The Liberia specimens differ from those of Sierra Leone only in the length of the caudæ of the corolla-lobes, which in the former appear to be longer and more setaceous in character (Wernham).

Both Scott-Elliot and Oliver compare this species with the two other *Vangueria* with caudate corolla-lobes: *V. velutina* Hiern, which has densely tomentose leaves and inflorescences; and *V. pauciflora* Schweinfurth, with solitary or geminate flowers and truncate calyx.

This species was evidently redescribed by K. Schumann, in 1897, as *Cuviera trichostephana*, on part of the material collected in Sierra Leone by Scott-Elliot. For the sake of completeness, Schumann's description of *C. trichostephana* is translated here:

A woody plant with slender, terete or subtetragonal branches, very glabrous even in youth. Leaves on the specimen examined not completely developed, petiolate, oblong, shortly and obtusely acuminate, acute at the base and often suboblique,

glabrous on both sides, but the axils of the veins with minute hairy domatia; stipules lineate-subulate, with triangular base. Axillary cyme with few flowers, glabrous; ovary 5-celled, glabrous; calyx with foliaceous or membranaceous, oblong, sharp lobes. Corolla divided to beyond its middle, with a corona of decumbent hairs inside, pilose at the outer side, with very long, crenate, linear-lanceolate lobes.

The branch at hand is 15 cm. long and at most 2 mm. thick at the base. The petiole reaches a length of 1 cm. and is slightly excavated above. The blade is 4 to 9 cm. long and 2 to 4 cm. broad in the middle; traversed by 5 stronger veins on each side of the midrib; black when dried; herbaceous in the specimen studied, but the leaves are apparently not yet fully developed. The stipules reach a length of 7 to 8 mm. The entire inflorescence is about 3 cm. long. The pedicels of the flowers reach a length of 5 mm. The ovary is semiglobose and 1.5 mm. long. The lobes of the calyx reach 10 mm. in length and 3 mm. in width. The corolla is 2.2 to 2.5 cm. long, of which the tube takes 9 to 10 mm. only. The anthers are 2 mm. long, placed on filaments 3 to 4 mm. long, exerted from the tube and curved. The style is 1.7 cm. long.

This species is easily separated from all others by the corolla covered with hairs, the smaller leaves, and the short inflorescences. It has more the appearance of the genus *Vangueria*, so that it makes the generic limits less distinct.

Sierra Leone (C. F. Scott-Elliott).

Cuviera physinodes K. Schumann

Cuviera physinodes K. SCHUMANN, 1891, Pringsheim's Jahrb. Wiss. Bot., XIX, pp. 55-56; 1891, in Engler and Prantl, 'Die Naturl. Pflanzenfam.,' IV, pt. 4, p. 12, fig. 5A.

Cuviera physinodes H. KOHL, 1909, Natur u. Offenbarung, LV, pp. 162-163.

"Leaves large, 20 to 30 cm. long, 7.5 to 11 cm. broad, with thick petiole, ovate-oblong or oblong, shortly and obtusely acuminate, equilateral at the base, coriaceous, glabrous on both sides. Ovary 5-celled; stigma glabrous. Drupe oblong, 3 cm. long, about 1 cm. in diameter, acute at the apex, acuminate at the base, without ribs.

"It is a tree-like shrub about 3 m. high, with large, leathery leaves. The cymes are axillary, with many flowers, short, ramified; only a few of the greenish white flowers produce fruit, though all seem to possess well-developed ovaries. The cylindrical internodes, covered with gray bark, are regularly thickened in their upper part, but do not develop swellings there. The swellings are situated rather above, and close to the nodes" (K. Schumann, 1888).

Gaboon: Sibange farm, type locality (Soyaux).

The myrmecodomatia of this species have been briefly described by K. Schumann from dried specimens. One of the hollow, nodal swellings had a length of 3.5 cm. and greatest diameter of about 1 cm., the wall being about 1.5 mm. thick. The inner cavity was nearly spindle-shaped and ended slightly below the node; three openings led into the cavity; one of these, 2 mm. long and 1.5 mm. broad, was probably alone used as entrance, while the two others were reduced to mere slits, 1 mm. long and hardly 0.5 mm. wide. Traces of former holes, evidently closed by callus growth, could be seen on two other spots. A few remains of ants were found inside the swellings.

Cuviera plagiophylla K. Schumann

Cuviera plagiophylla K. SCHUMANN, 1903, Engler's Bot. Jahrb., XXXIII, p. 353.

"A shrub with thick, fistulose-inflated branches, which, even when young, are glabrous. Leaves strictly sessile, linear-oblong, short acuminate, rounded at the base, strongly inequilateral, glabrous on both surfaces. Stipules tubular, villose internally. Flower panicle axillary, with many flowers. Bracts very long, linear, acuminate. Ovary 5-celled. Sepals free almost to their base, linear, acute. Corolla with very short tube; the lobes acuminate, moderately appendiculate, cristate dorsally. Style glabrous.

"The bush reaches a height of 5 m. The leaves are 28 to 30 cm. long and 8 to 9 cm. broad; they are crossed on each side of the midrib by about 16 stronger veins, which are more prominent on the under side, as are also the reticulate veins; they are black when dry. The stipules are 9 mm. long. The lobes of the calyx are 11 mm. long and somewhat obtuse. The corolla is greenish-white, 15 mm. long, of which 2 mm. is to be allowed for the tube; the appendages measure 5 mm.; the keels on the dorsal face of the lobes make the bud sharply 5-ribbed.

"The species is very distinct by the strictly sessile, very oblique leaves and the acutely keeled corolla-lobes" (K. Schumann, 1903).

Cameroon: Bipindi, near Lokundje (Zenker).

Cuviera subuliflora Benth

Cuviera subuliflora BENTHAM, 1849, in Bentham and Hooker, 'Niger Flora,' p. 407.

HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 157.

"An arborescent shrub or small tree of 15 feet, glabrous. Branches subterete, smooth, opposite. Leaves oblong, shortly acuminate, oblique and hollowed or rounded or somewhat narrowed at the base, chartaceous, rather paler beneath, 6 to 15 by 2 to 4 $\frac{3}{4}$ in.; lateral veins about 12 to 14 pairs, slender; petiole $\frac{1}{4}$ in. long; stipules deltoid, connate at the base, keeled near the apiculate apex, $\frac{1}{4}$ to $\frac{1}{2}$ in. long, hairy within. Flowers numerous, on short pedicels, in divaricately branched axillary and lateral, subsessile, dichotomous panicles of 2 to 3 in. diameter; bracteoles linear, narrowed at both ends, $\frac{1}{2}$ to 1 $\frac{1}{2}$ in. long, accrescent as well as the calyx-segments. Calyx whitish; segments narrowly or at length broadly linear, ranging up to 1 in. long. Corolla green; segments about $\frac{1}{2}$ in. long, lanceolate, caudate-acuminate. Style glabrous. Ovary 5-celled. Fruit 1 in. long, obliquely egg-shaped" (Hiern, 1877).

Fernando Po: on the sea shore (Vogel).

Southern Nigeria: Abo (Vogel).

Cuviera trilocularis Hiern

Cuviera trilocularis HIERN, 1877, in Oliver, 'Flora of Tropical Africa,' III, p. 157.

"A small glabrous tree. Branches subterete, smooth. Leaves ovate-oval, acuminate, rounded and suboblique at the base, thinly coriaceous, glossy, of nearly the same color on both sides, 4 to 5 by 1 $\frac{3}{4}$ to 2 in.; lateral veins about 8 to 10 pairs; petiole $\frac{1}{2}$ to $\frac{1}{3}$ in.; stipules apiculate, ovate, keeled, $\frac{1}{2}$ in. Flowers on short pedicels, several together, in the terminal or subterminal axils; panicles 1 $\frac{1}{2}$ to 2 in. diameter; common peduncle about $\frac{1}{2}$ in., bracteoles lanceolate, $\frac{1}{2}$ to $\frac{3}{4}$ in. long. Calyx-segments greenish white, $\frac{1}{2}$ in. long or rather more, linear-elliptical, acute, narrowed toward the base. Corolla shorter than the calyx; lobes lanceolate, caudate-acute. Style glabrous; stigma 10-sulcate. Ovary 3-celled" (Hiern, 1877).

Southern Nigeria: Old Calabar (W. C. Thomson).

ECOLOGY OF *Cuviera* IN THE BELGIAN CONGO

The representatives of this genus observed by me mostly occurred in low-lying or moist places, though not in those apt to be frequently flooded; raised river banks are favorite sites. Usually growing as shrubs or bushes, 2 to 4 meters high, under favorable conditions they may become small, pyramidal, bushy trees of 5 to 7 meters. The trunk is slender, erect, and destitute of branches below where it often, but not always, bears opposite, decussate, very sharp spines, 2 to 5 cm. long. The long, slender branches spread more or less horizontally and their tips hang down somewhat. In accordance with the decussation of the leaves, they are placed opposite each other in four regular rows. As a rule the upper part of the plant is unarmed, though in some specimens one finds in the axils of the leaves heavy, straight spines, evidently modified, aborted branches.¹ The leaves are very large, 10 to 25 cm. long, 5 to 11 cm. broad, borne on a short petiole (of about 1 cm.), entire and simple, thinly coriaceous, smooth and glabrous on both sides, dull green above, paler below; usually cuspidate or more or less acuminate at the apex, oblique and rounded or slightly heart-shaped at the base. The lateral nervures are rather thin, more conspicuous on the under side of the leaf, and number 8 to 10 on each side of the midrib. The stipules are connate into a short, loose sheath, which is keeled, acuminate, and about 0.5 to 1.5 cm. long. The base of this stipular sheath persists on older branches.

The plant is not often seen blossoming. Welwitsch, in Angola, found flowers in April and May and fruits in August; while in the Belgian Congo, flowering specimens were seen by Dewevre in March (Lukolela) and by me in February (Penge), July (Kunga), and December (between Masisi and Walikale); fruits were found in January, 1915, between Walikale and Lubutu on a plant not in flower. From these very incomplete data, which may relate to different species, it would appear that *Cuviera* blossoms from December to July, yet it is quite possible that there is no definite flowering season, as is so often the case with bushes and trees of tropical rain forests.

Dewevre in his field-notes accurately describes the flowers of *C. angolensis*. They are large, conspicuously colored, and placed as many as a dozen together in axillary, polygamous panicles, toward the upper end of the younger branches. The common peduncle is 0.5 to 4 cm. long, while the pedicels are very short, the flowers being subsessile in the axils

¹Kohl (1909, p. 164) and De Wildeman (1906, p. 297) also note that the branches of certain specimens of *Cuviera angolensis* are unarmed, whereas in others they are spinose. There is a possibility that these differences are of specific value.

of slender and narrow bracteoles of about 2.5 cm. The calyx is pale green, deeply cut into 3 to 5 elongate-lanceolate lobes, extending far over the corolla, and 1.5 to 7.5 cm. long. The corolla is short salver-shaped (hypanthioid), fleshy coriaceous, mostly deep green; the tube is short, bright carmine red, which color extends as a median acuminate line or triangular spot over the upper side of each of the five lobes. These five corollar lobes are lanceolate or oval-acuminate, rigid, and spread into a star when in full blossom. The tube of the corolla bears inside a ring of silvery, shiny hairs directed downward. The five stamens are exserted, placed in the sinuses of the corollar lobes, around the ring of hairs; their filaments are slightly flattened, fleshy, carmine red; their anthers are yellow. The style is thick, columnar, carmine red, densely white pilose, and ends in a large, obtuse, cap-shaped, pale green stigma. Frequently the fruit is oblique or even curved and falcate; but this is due to the aborting of one or more of the ovules; when the fruit is normally developed it is an obovate, dirty yellow drupe, about 23 to 32 mm. long and 18 to 25 mm. thick; its surface is deeply furrowed, there being 5 heavily developed ribs with less prominent ones between them; the ripe fruit is crowned with the remains of the withered calyx. It is noteworthy that very few of the flowers produce fruit.

Cuviera angolensis was recognized as a myrmecophyte by K. Schumann (1890, p. 121), who found unidentified ants in the domatia of Welwitsch's herbarium specimens. The first field-notes on this plant were made by Dewèvre in 1896 (De Wildeman and Durand, 1900, p. 124) and these were completed by Em. Laurent (De Wildeman, 1916, pp. 296-299) and H. Kohl (1909, pp. 163-166). Their accounts agree in almost every detail with my own observations on Congo *Cuviera* as reported below. The following ants are known from *C. angolensis*.

Crematogaster africana (Mayr). Romée (H. Kohl, 1909, p. 164; Forel, 1909b, p. 69).

C. africana subspecies *laurenti* (Forel). Romée (H. Kohl, 1909, p. 164; Forel, 1909b, p. 69). In that locality the coccid *Stictococcus formicarius* Newstead was living inside swellings of *C. angolensis* also occupied by this ant (Newstead, 1910, p. 19).

C. africana subspecies *winkleri* (Forel). Eala (Em. Laurent; see Forel, 1909b, p. 69).

Cuviera angolensis Hiern was the only member of the genus recorded from the Belgian Congo, where it is far from rare. I had opportunity to examine in several localities a number of *Cuviera*, all

of which at the time I regarded as belonging to this species, since they agreed with its description. While studying the anatomy of *Cuviera*, Prof. Bailey discovered certain histological dissimilarities between specimens collected at different places, yet it is possible that these discrepancies are due either to the difference in the age of the various branches or to their mode of preservation. In view of the fact that the number of African species has been so increased recently, the *Cuviera* of the Congo Basin will need considerably more field study before their identity can be safely discussed. Meanwhile, my notes are presented separately for each of the specimens I examined.

1.—At Avakubi (January 6, 1914; Coll. No. 1796) a *Cuviera* was found growing on the banks of the Ituri River. It was a low bush (4 to 5 meters high), well answering the general description given above, but without flowers or fruit; flower buds were, however, noticed a few days later on another specimen in the same locality. The trunk was cylindrical, and neither swollen nor hollow. Most of the branches showed at each node a spindle-shaped swelling which extended over the lower two-thirds to three-quarters of the internode, and was about 8 to 10 mm. thick and 6 to 7 cm. long. Notwithstanding the fact that expanded portions were almost completely hollow, their solid, woody walls made them very resistant to pressure. They were present even on young limbs and early became hollow, through the drying of the medullary tissue, before being attacked by ants.

On some of the branches the swellings contained a beetle larva feeding on the remains of dried pith, but there was always an orifice by which the insect had entered the stem. Some of these beetle larvae were accompanied by coccids, though no ants were associated with them in the cavity. This is of great interest because it shows that the coccids enter the domatia of their own accord as soon as an aperture is pierced.¹

The majority of the swellings of older limbs were inhabited by ants of different species, the most common being an unidentified *Crematogaster*. I further collected in other domatia of the same plant *Cataulacus pilosus* Santschi and *Technomyrmex hypoclinooides* Santschi. All of them had established in the cavities regular formicaries with larvae and pupae. In the case of the swellings tenanted by *Crematogaster*, each sheltered a separate colony, with its own queen, a number of workers, and abundant brood. Furthermore, the younger swollen internodes on the upper end of the branches were often occupied by a solitary queen, some-

¹Kohl (1909, p. 165) also mentions the presence of an insect larva, together with scale insects, in some of the swellings of *Cuviera angolensis*.

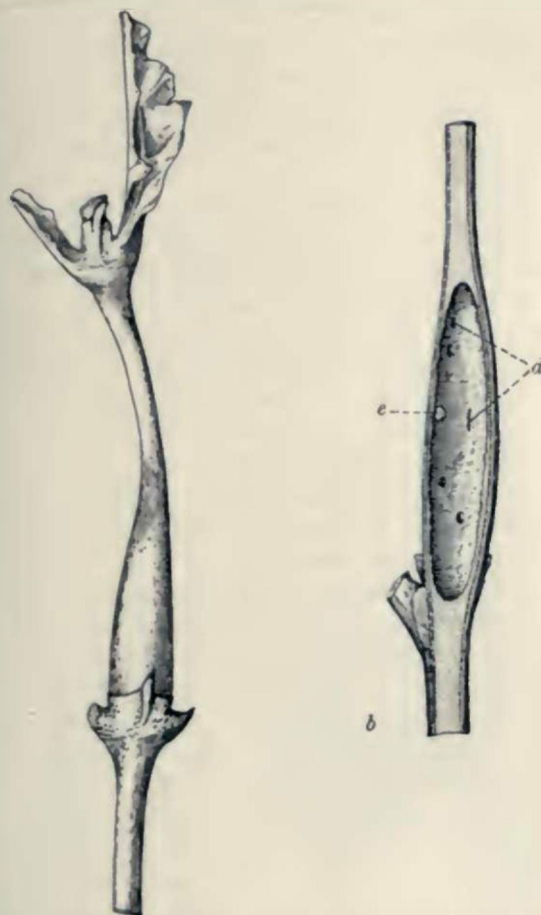


Fig 99. *Curiera angolensis* Hiern: *a*, upper portion of branch with one of the caulinary myrmecodoma above the node; *b*, longitudinal section of one of the swellings; *e*, aperture gnawed by the ants and leading into the cavity; *d*, pits often occupied by coccids. Drawn from alcoholic specimens collected at the Tshopo River, near Stanleyville; natural size.

times in company with a few coccids, the exit hole being partly closed by callus growth. Working down the branch, one frequently met with all stages in the development of the colony, ending with the appearance of the winged, sexual phases. It thus appears that the various colonies in a single *Curiera* do not fuse into one great community as is the case with the *Pachysimæ* of *Barteria* and the *Viticolæ* of *Vitex Staudtii*, yet they manage to live peacefully side by side.

The three species of Formicidæ found in this *Cuviera* were small and timid, and showed no aggressiveness, remaining inside the domatia when the plant was disturbed. They could not have been of much value as guards against phytophagous insects or other enemies. Indeed, numerous leaves of a specimen densely populated by ants were noticeably eaten by caterpillars.

2.—A *Cuviera* found at Penge (February 13, 1914; Coll. No. 2461), along the Ituri River, agreed in every particular with the specimens from Avakubi described above. It was in full bloom and all of its swellings were occupied by an unidentified *Crematogaster*.

3.—Another *Cuviera* collected near the village of Masaki, between Masisi and Walikale (December 31, 1914; Coll. No. 6429), also agreed entirely with the plants from Avakubi. Its swellings were occupied by two different ants, *Engramma denticulatum* Wheeler and *Tetramorium meressei* Forel, each in domatia of its own.

4.—The above remarks further apply to a *Cuviera* collected in fruit near Sitaweza, between Walikale and Lubutu (January 13, 1915; preserved in my herbarium without Coll. No.). In this case the inhabitants were *Crematogaster excisa* subspecies *andrei* (Forel).

5.—Along the Tshopo River, near Stanleyville, Mr. H. Lang and I collected, March 8, 1915, much material of *Cuviera* which was abundantly settled by the ant *Crematogaster africana* subspecies *laurenti* variety *zeta* (Forel). Figure 99, drawn from alcoholic specimens, shows the outer and inner structure of the domatia, which were in every respect similar to those of the plants observed at Avakubi, Penge, Masaki, and Sitaweza. Prof. Bailey states that, compared with the swellings of the Kunga specimens, those of the plants from the Tshopo are "shorter, slimmer, and of a deep olive green color"; in addition, the cortex and bast are relatively free from "amber-colored substance" and the pith cells which contain this substance are diffused, with a peripheral row scattered along the inner margin of the stele. These Tshopo examples are referred to as "*Cuviera angolensis*" in Prof. Bailey's anatomical studies (Part V, p. 593).

6.—At Kunga, north of Malela, Mr. H. Lang and I found a *Cuviera* (July 11, 1915; Coll. No. 7983) inhabited by numerous ants, *Crematogaster impressiceps* variety *frontalis* Santschi. The myrmecodomatia (Fig. 100) are longer and broader than in the specimens from the Tshopo River and of a reddish green color. The histological structure of the stem is also somewhat different; the "amber-colored substance" is concentrated in the subepidermal and other cortical cells, whereas the

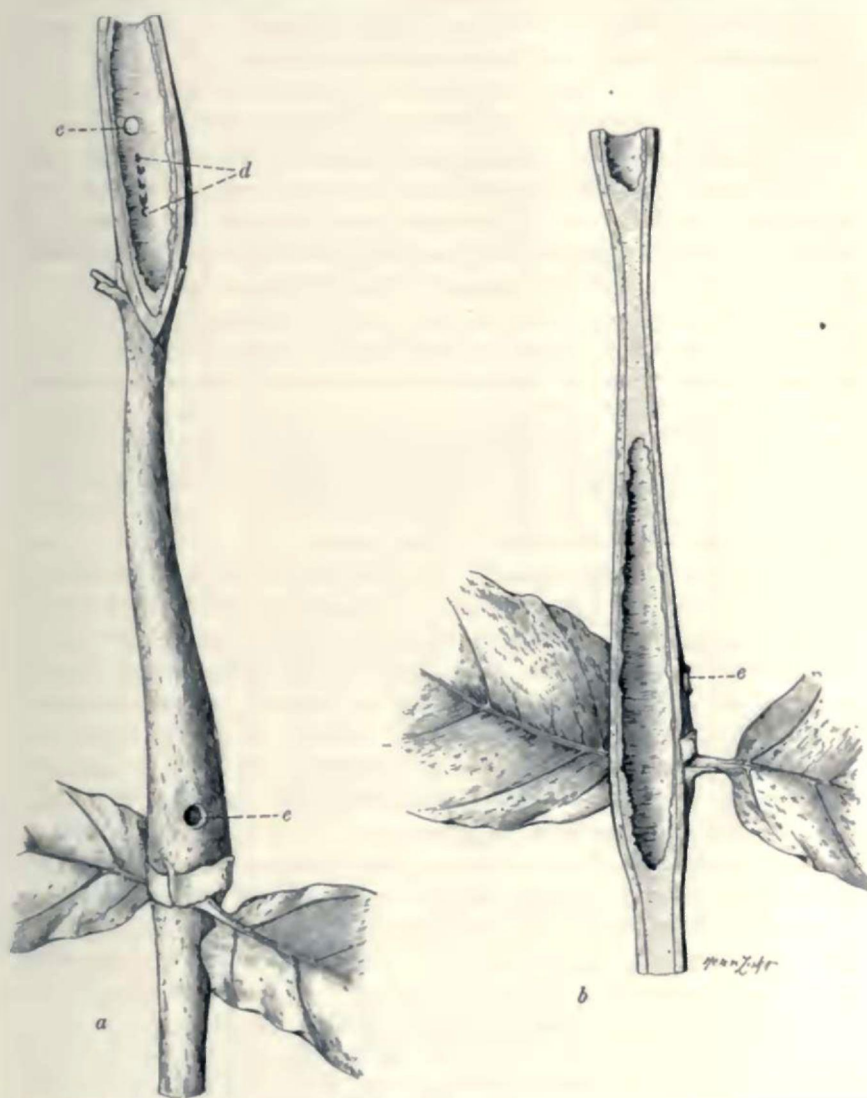


Fig. 100. *Cusiera* species? a, portion of branch giving external view of one of the domatia and the longitudinal section of another; b, longitudinal section of one of the domatia; c, aperture gnawed by ants; d, pits often occupied by coccids. Drawn from herbarium specimens obtained at Kunga, near Malela; natural size.

pith cells containing it are aggregated in the center of the more deeply lobed medulla (Bailey). The plant from this locality is referred to as "unidentified *Cuviera*" in Prof. Bailey's contribution (Part V, p. 593).

3. SYNOPSIS OF RECORDED MYRMECOPHYTES

The study of ant-inhabited plants is in such an incomplete state that no adequate or standard definition of the term "myrmecophyte" has so far been formulated. The student must therefore be prepared, in reading the present synopsis, to meet with cases of very unequal value. Warburg (1892, p. 130) has proposed to classify plants according to the nature of their relations with ants into the following three groups:

a. MYRMECOTROPHIC plants provide only food to the ants, either in the form of sugary exudates (nectaries,) special food-bodies (bromatia of the fungi), seeds or fruits of the myrmecochores, and the like.

b. MYRMECODOMIC plants furnish only shelter to the ants' nests, either in normal cavities, such as hollow stalks, or in special swellings or myrmecodomatia.

c. MYRMECOXENIC plants act as true hosts, offering to their ant guests both shelter and food. Typical cases of the kind are *Cecropia adenopus* (with the Müllerian bodies) and *Acacia cornigera* (with the Beltian bodies).

The term "myrmecophyte" is here used to include Warburg's "myrmecodomic" and "myrmecoxenic" plants. A further distinction of these two categories seems very unwise at present, because we are, it appears, just beginning to understand the true relations existing between ants and the plants they inhabit. My definition of "myrmecophytes" is based on practical considerations and is thus merely provisional. In the main, however, I agree with Ule (1906b, p. 335), who proposes to designate as ant-plants all plants which are steadily inhabited by certain species of ants, excluding only cases where the ants occasionally settle in normal leaf-sheaths, slits in the bark, dead branches, etc. Schumann's (1888) definition, on the other hand, is quite teleological and therefore of little use under present circumstances, since he wishes to restrict the term "myrmecophyte" to those plants "that are not merely visited by ants, but are purposely inhabited by them, and that therefore have probably entered with them into a true symbiotic relation."

The exquisite manner in which many ants have come "to know plants" (Michael Gehlerus, 1619) must indeed astonish the botanist who is but little acquainted with the psychic activities of these tiny insects. In his search for a much-needed explanation he naturally turns to the magic action of "Natural Selection," following in this the general trend of present ecological botany. Various theories of myrmecophytism are fully exposed and critically discussed by Prof. Bailey in part V of this

Report (pp. 610-614), so that a further consideration of this interesting topic is unnecessary here.

The origin of the various plant structures used by ants for nesting or feeding purposes is a purely botanical problem.¹ To the myrmecologist, on the other hand, belongs the task of tracing the various modifications of ant behavior which have gradually led to the close, obligatory cœnobiotic associations of certain Formicidæ with certain plants. It is not difficult to show that here, as elsewhere, the specialization in the habits of ants has followed its own course, quite independently of any simultaneous changes in the structure of plants.

Numerous ants belonging to many genera of the higher groups, viz., the Pseudomyrmicæ, Myrmicinæ, Dolichoderinæ, and Formicinæ, establish temporary shelters or permanent colonies in dead branches, stumps of trees, dry stalks of herbs, and like places. In what perhaps may be regarded as the most primitive stage of this behavior, the ants merely appropriate existing cavities, such as old burrows of wood-boring larvæ, empty galls, and hollow pith channels. Dry stalks of grasses, reeds, and other herbaceous plants are also great favorites as nesting sites with many tropical ants (Forel, 1896a-d). At Luali, Belgian Congo, I found in August, 1913, a beautiful and populous nest of a *Camponotus* established in a dry stalk of papyrus on the bank of the Shiloango. Tucker (1911, pp. 24 and 26) mentions finding nests of the North American *Crematogaster lineolata* Say subspecies *læriuscula* Mayr variety *clara* Mayr, at Alexandria, Louisiana, in corn-stalk cavities formed by a borer and also in hanging "bolls" or fruits of cotton. The common *Lasius niger* (Linnaeus) was observed in Europe in fallen apples, temporarily occupying the empty galleries made by the apple-moth (Ruzsky, 1913, pp. 61-63).

In many cases ants excavate new galleries in dead or decaying vegetable tissues or transform the fibres into "carton" used as partitions or plugs. One of the most typical of these borers in dead wood is

¹In a recent publication, Chodat and Carasso (1920) argue that the caulinary swellings of myrmecophilous plants are mere galls caused by the sting of insects and subsequently settled by the ants. They base their conclusion on the fact that they found insect larvæ in various stages of development inside the swellings of *Cordia glabrata* de Candolle, *C. longituba* Chodat and Vischer, and various other species of this genus, and also inside the swollen stipular thorns of *Acacia casentia* Hooker and Arnott. This view, however, has not found much favor with other investigators (see De Wildeman, 1921). In the cases of the African *Barteria fistulosa*, *Curiera*, *Plectronia Laurentii*, *Randia myrmecophyla*, etc., there can be no question but that the myrmecodomatia are normal, hereditary organs of the plant and that insects take no part in their production. This is undoubtedly also true for the swollen thorns of the Central American bull-horn acacias, which reach their characteristic size and shape even under cultivation. It must further be pointed out that the mere presence of insect larvæ feeding inside plant swellings does not necessarily mean that these swellings are galls made by the insects, whose occurrence there may be purely accidental. Many years ago Viebrig (1909) noticed that caterpillars frequently destroy the pith of the swollen thorns of *Acacia casentia*. Moreover, that insect galls have been and still are mistaken for true myrmecodomatia has been shown elsewhere (pp. 371-375), so that each particular case must be examined with the utmost care, in order to ascertain its true standing.

the common *Camponotus caryæ* (Fitch), several forms of which occur throughout the Palearctic and Nearctic Regions (Wheeler, 1910c, pp. 219-220). Many species of *Crematogaster* and *Leptothorax* remove the pith from dead twigs of trees, briar and rose bushes, etc., to make homes for themselves (Forel, 1903b; Stager, 1917 and 1919).¹ A peculiar cœnobiotic association was described by Wheeler (1912a) in the case of a mistletoe, *Phoradendron flavescens* variety *villosum* Nuttall, which grows on live oaks (*Quercus emoryi* Porter and Coulter) in the Huachuca Mts., Arizona. The branches of this mistletoe are very frequently hollowed out for some distance by a curculionid larva; the beetle makes its exit through a round hole at the side of the twig and the deserted gallery is then usually occupied by a colony of *Crematogaster arizonensis* Wheeler. Furthermore, the walls of these formicaries are invariably covered with reddish coccids, *Pseudococcus phoradendri* Cockerell. In the tropics of both hemispheres, many species of *Cataulacus* (Paleotropical) and *Cryptocercus* (Neotropical) are true wood-boring ants. Similarity in habits has gradually resulted in a remarkable resemblance in the shape of the head and the flattened body of these two genera, though they are not closely related to each other.

The keenest carpenter ants, such as the holartic *Camponotus herculeanus* (Linnæus), with its various races and varieties, and the European *C. vagus* (Scopoli), frequently extend their burrows into the live, healthy wood of standing timber. It is, however, among the tropical and subtropical Pseudomyrminae that we find all transitional stages between the common wood-boring habit and the more specialized behavior of nesting inside living, normal organs of plants and myrmecodomatia. The impulse to gnaw through living vegetable tissues not only presupposes a greater inquisitiveness on the part of the ants, but it is undoubtedly also influenced by the anatomical structure and chemical composition of the plant, as is clearly shown by Prof. Bailey's histological study of myrmecophytes (See Part V, p. 585-621).² From the habit of boring into normally existing cavities of plants it is only a step to the excavating

¹In January, 1910, I found several nests, with queens and workers, of *Leptothorax angustulus* (Nylander) variety *brunneus* Santachi inside dead, hollowed stalks of wild roses near Algiers. The common North American *L. curvispinosus* Mayr usually nests in hollow twigs or stalks.

²The larvae of many Hymenoptera, such as the Tenthredinidae and Siricidae, most Cynipidae, and certain Chalcididae, are phytophagous, feeding on the living tissues of healthy, growing plants. It may not be so commonly known that as adults, too, some of them attack living parts of plants. Certain of the larger saw-flies are known to injure twigs of bushes by girdling them with their mandibles. The large hornet, *Vespa crabro*, gnaws the new bark of trees in order to get building material for its paper nests. A number of tropical and subtropical bees and fossorial wasps are known to excavate nesting galleries in the green, juicy pith of living plants. According to Brauns, this is one of the peculiarities in the behavior of certain South African *Xylocopa*, *Ceratina*, and *Dasyprotus*. I have observed similar habits in species of *Allodape* and *Dasyprotus* in the Belgian Congo. Bertoni, in Paraguay, found *Xylocrabro umbrosus* S. Hottky nesting in the green stalks of radish which ripens its seed about the time the young wasps are hatching.

of the pith of living branches, which brings us then to the settling of the so-called myrmecodomatia. That pith-nests, such as those described for *Endospermum formicarum* Beccari by Dahl (1901) in New Guinea, have been so seldom noticed is probably merely due to a lack of proper investigation.

In the following pages an attempt is made to review the various cases of true myrmecophytism which have thus far been recorded, as the pertinent observations are quite scattered in entomological and botanical publications. In this list the plants are arranged according to their systematic sequence. I have added a few remarks on distribution, a short description of the myrmecodomatia, and a record of the ants found therein. The available information is, however, often very scanty. So far as possible, doubtful or erroneous observations have been excluded or expressly questioned, while the recording authors are given in each case. The dates refer to the appended bibliography.

PTERIDOPHYTA

Polypodiaceæ

A cosmopolitan family, containing some 100 genera and 2800 species.

Polypodium Linnaeus. Cosmopolitan, with about 200 species; some of the Oriental species are well-known myrmecophytes.

P. sinuosum Wallich. Malay Region from Malacca to the Solomon Islands. Inhabited by *Technomyrmex albipes* (Smith), an ubiquitous ant (Yapp, 1902; Ridley, 1910; Shelford, 1916); also by *Iridomyrmex myrmecodix* Emery in Borneo (Wheeler, 1919, p. 100) and in Java (Miche, 1911b), and by *I. cordata* (Smith) in New Guinea (Beccari, 1884).

P. lomarioides Kuntze. Malay Region (Yapp, 1902).

P. sarcopus De Vriese and Teysmann. Celebes (Yapp, 1902).

P. imbricatum Karsten. Amboina.

P. leiorhizon Wallich. Eastern Himalaya, Western China.

These five species constitute the subgenus *Aspidopodium* Diels (= *Myrmecophila* Christ). They are epiphytic ferns, with creeping, semicylindric rhizomes, which are fleshy and much swollen on the upper side where the leaves are inserted on mammary protuberances; the flattened under side is pressed against the support. Originally the swelling is filled with an abundant aquiferous tissue, which in drying up causes the rhizomes to be tunnelled almost their whole length. The resulting cavities are, as a rule, inhabited by ants which pierce the entrances (Græbel, 1888; G. Karsten, 1895).

A species of *Polypodium* (?*P. megalophyllum* Desvaux = *P. Schomburgkianum* Kuntze) of South America (Rio Negro; Rio Napo) is said to have rhizomes similarly swollen and occupied by ants. A Costa Rican species, *Polypodium Brunei* Wreckle, possesses small bulbs, about 2 to 2.5 cm. in diameter, fixed by short peduncles at the sides of the rhizome; these bulbs are hollow, provided with an orifice, and divided by partitions into four or five spacious chambers. G. Senn (1910) regards them as water reservoirs; whether they are occasionally inhabited by ants is not known. *Polypodium bifrons* Hooker, of Brazil, has similar swellings which, according to Ule (1906b), act also as water reservoirs and are not occupied by ants.

Lecanopteris Blume. Malay Region. Represented by four or five closely allied species, all epiphytes, with swollen, tuberiform rhizomes, traversed by a system of galleries inhabited by ants. The genus is doubtfully distinct from *Polypodium*.

L. deparioides (Cesati). Borneo (Shelford, 1916).

*L. carnos*a Blume (= *Polypodium patelliferum* Burek). Perak, Borneo, the Moluccas, Philippines, Celebes, Java (Yapp, 1902; Ridley, 1910; Shelford, 1916). Inhabited by *Crematogaster yappii* (Forel) and *C. difformis* F. Smith. Hooker believed that *L. carnos*a represented a teratological condition of *Polypodium lomarioides*, but this view has been discarded following Burek's (1884a) observations of this plant.

L. Curtisii Baker. Sumatra.

L. Macleayii Baker. Java.

Some of the Old World epiphytic ferns of the genus *Drynaria* Bory have been improperly included among the myrmecophytes. They are remarkable in having, in addition to the normal, fern-like leaves, others which are sessile, broad, superficially divided, and pressed against the support and the rhizome. Humus accumulates underneath the cover of these appressed leaves and is soon invaded by roots. Frequently ants nest in this humus, but their presence there is merely accidental and I agree with Gœbel (1888) that these cover-leaves ("Nischenblätter") can by no means be considered as myrmecodomatia. *Drynaria Laurentii* Christ is one of the commonest epiphytic ferns of the Congo Basin and shows all the peculiarities of the genus beautifully. *D. quercifolia* (Linnaeus) is abundant in the Oriental Region, from India to Polynesia.

Pheidole javana Mayr subspecies *jacobsoni* Forel variety *taipingensis* Forel was found by v. Buttel-Reepen forming small colonies in the cavities of the irregularly thickened root of an epiphytic fern in Malacca

(Forel, 1913, p. 28). More details concerning this plant will probably be given in v. Buttel-Reepen's forthcoming paper on the biology of East Indian social insects.

MONOCOTYLEDONEÆ

Palmæ

An abundant family in tropical and subtropical regions, especially in South America and the Malay Region. Approximately 170 genera, with 1200 species, have been described. A small number of species have been found associated with ants but, with the exception of certain *Korthalsia*, they can hardly be called myrmecophytes.

Korthalsia Blume. Oriental Region. With twenty species, all of which are rattan-palms. While the ligule of the leaf-base usually forms a close, tightly fitting sheath, in a few species which constitute a special section, this organ is dilated into a rounded or oblong, bulky sheath or ocrea of a stiff papery texture, frequently perforated and occupied by ants of the genus *Camponotus*. Emery has expressed the opinion that these *Camponoti* belong to a special group of the genus, adapted to living in the ocrea of these palms.

K. scaphigera Martius. Malay Region (Beccari, 1884; Ridley, 1910; Shelford, 1916). In Sumatra Beccari found the ocrea of the leaves perforated on the sides and inhabited by *Camponotus hospes* Emery; in Borneo a related *Camponotus* was found in this palm. According to Ridley (1907, p. 216) the natives of the Malayan Peninsula call this palm "Rotan semut" or ant-rattan.

K. echinometra Beccari. Malay Region (Beccari, 1884; Ridley, 1910; Shelford, 1916). The ant found in Sarawak in this palm by Beccari was *Camponotus contractus* Mayr, which had cut an entrance. On passing near the plant one may hear the ants running along the walls of the ocrea, which acts as a resonator. Emery (1888, p. 529, footnote) described *C. contractus* variety *scortechinii* from specimens taken in the ocrea of *K. echinometra* in Perak. *Crematogaster difformis* F. Smith had settled in the ocreæ of specimens of this palm cultivated at Buitenzorg; it had not pierced an orifice, as did the *Camponotus* mentioned above, but merely made its way along the slight depression near the upper margin of the ocrea.

Camponotus contractus variety *buttesi* Forel, from Kuala Lumpur, Selangor (Malacca), was found in the hollow swellings of a plant called by the natives "Rotan udang," in which the workers make a peculiar noise at night (Forel, 1902, p. 463). According to Ridley (1907, p. 216), this is the Malayan name of *Korthalsia echinometra*.

K. angustifolia Blume. Malay Region. In Sumatra, Beccari found the ocreæ pierced with a hole and inhabited by *Camponotus korthalsiæ* Emery (Beccari, 1884).

K. horrida Beccari, *K. Scortechinii* Beccari, and *K. cheb* Beccari, all from the Malay Region, have a similarly constructed ocrea, with an orifice undoubtedly pierced by ants which have not been identified (Beccari, 1884).

Calamus Linnæus. About 150 species in the Oriental Region from India to tropical Australia and Polynesia; one species in tropical Africa.

C. amplexans Beccari. Borneo. The two lower segments of the leaves are folded back and embrace the stem so as to enclose it, the resulting cavity being inhabited by ants (Beccari, 1884; Shelford, 1916).

Dæmonorops Blume. Oriental Region. Represented by seventy species, all rattans. In several of them ants habitually make nests in the large, stiff flower-spathes, which often quite cover the flower-panicles. The genus is closely allied to *Calamus*.

D. Jenkinsianus Martius. Malay Region. Flower-spathes inhabited by a *Camponotus* allied to *C. mitis* (F. Smith) (Ridley, 1910).

Orchidaceæ

One of the largest families of plants, containing 500 genera and over 15,000 species. Cosmopolitan, but chiefly in warm and humid regions. The following cases of myrmecophytism are still doubtful and need closer investigation.

Diacrium Lindley. Epiphytes of the Neotropical Region; four species.

D. bicornutum (Hooker), of Trinidad and Guiana, has a swollen, spindle-shaped stem, which is normally hollow and perhaps regularly inhabited by ants (Rodway, 1911, p. 111). Schlechter¹ claims that even under cultivation the pseudobulbs form at their base a slit through which the ants gain access into the cavity.

Schomburgkia Lindley. Epiphytes of the Neotropical Region. Represented by thirteen or fourteen species, from Mexico to Guiana and Peru, several of which have hollow pseudobulbs.

S. tibicinis (Bateman), in Central America (from Mexico to Venezuela), has voluminous, elongated pseudobulbs, which are hollow, with a smooth inner lining and usually inhabited by ants; these go and come through a small opening pierced at the base of the pseudobulb (Ross,

¹"Die Orchideen," (Berlin), 1915, p. 214.

1909; O. Massias, 1901; the plant is represented on Pl. xxxiv of Step, 1913). This is apparently a true myrmecophyte. Mayr (1862, p. 720) has recorded *Neoponera villosa* (Fabricius) from the pseudobulbs of this orchid at Vera Cruz, Mexico.

Grammatophyllum Blume. Epiphytes of the Malay Region; four species.

G. speciosum Blume is one of the largest orchids known; the stem reaches a height of 4 m. and is thickened, especially towards the base; occasionally it shows galleries occupied by ants.

DICOTYLEDONEÆ

Moraceæ

Cosmopolitan family, though chiefly tropical, with 70 genera and about 1000 species. The only myrmecophytic members known with certainty belong to *Cecropia*. Schimper has described and figured *Ficus inæqualis* with swellings, supposed to be myrmecodomatia, on the branches, but Ridley (1910, p. 458) has shown that these swellings are accidental, pathological productions.

Pourouma guianensis Aublet, of South America, which is related to *Cecropia*, according to Rettig (1904), possesses trichilia at the base of the petiole which produce food-bodies similar to the "Mullerian bodies" of *Cecropia adenopus*; whether they are collected by ants is not known. Forel (1904b) mentions *Azteca duroixi* Forel as having been found by Ule in the twigs of an unidentified *Pourouma* in Brazil.

Cecropia Linnæus. This genus occurs throughout tropical America from Mexico to Brazil. There are thirty to forty species, apparently very few of which (subgenus *Aztecopia* H. v. Ihering) are myrmecophytes. These latter shelter nests of various species of *Azteca* inside their hollow stems and also produce food for the ants in the form of so-called "Mullerian bodies." Many other species of this dolichoderine genus of ants nest in various locations or even build free carton nests in trees. It seems, however, that the species which inhabit the *Cecropiæ* are obligatory plant ants, being met with only inside these plants; the colonies perish when the trees die or are cut down.

Alfaro found inside the stems of an unidentified *Cecropia* in Costa Rica the following ants: *Azteca caruleipennis* Emery, *A. alfaro* Emery, *A. xanthochroa* (Roger), and *A. constructor* Emery (Emery, 1896b). Ule collected in Brazil *A. alfaro* subspecies *cecropiæ* Forel from another species of *Cecropia* (Stitz, 1913a). Warming (1894) studied in Venezuela a species of *Cecropia* which he found inhabited by *Azteca instabilis* (F. Smith).

Cecropia adenopus Miquel (= *C. peltata* Vellozo, nec Linnæus). A common species on the east coast of Brazil between 28° S. lat. and the Equator (H. v. Ihering, 1907). The best account of this celebrated plant is given by Wheeler (1910b, pp. 305-310):

The tree known as "imbauba" or "imbauva" is very slender and candelabra-shaped, growing to a height of 12-15 m. The trunk and branches are hollow except at the nodes, where there are thin transverse septa. The sap is colorless, not milky nor rubber-containing, as stated by some authors. The crown of foliage is meagre and consists of large, palmately lobed leaves. At some time of its life each node bears a leaf, the long petiole of which has at its base a hairy cushion, known as the trichilium, in which the yellow Müllerian bodies are imbedded. The cavities of older and larger trees are almost without exception tenanted by *Azteca muelleri* Emery, which perforates the septa and thus causes all the internodal cavities to communicate with one another, both in the trunk and branches. The ants do not, however, live in the smallest, still actively growing twigs. The just-fecundated queen enters the branches while the tree is still young (50 cm. to 2 m. high) at a particular point, a small depression at the upper end of a furrow at the top of the internode, where, as Schimper has shown, the wall lacks the fibrovascular bundles and is most easily perforated. Von Ihering calls the depression the "prostoma," the perforation which is formed in it the "stoma." The queen thus enters the internode by making a stoma and feeds on the tissue ("stomatome") which, according to von Ihering, soon proliferates over and closes the opening from the inside. In the small internodal cavity the first workers, six to eight in number, are reared, and these restore communication with the outside world by again opening the stoma.

Several females may each start a colony in one of the internodes of the same tree. Since later only one colony is found in a tree, v. Ihering supposes that the various primary colonies fuse to form one large community, after all except one of the queens have been killed. Such a fusion of workers from different colonies is, however, doubted by Wheeler. After the single community has grown and has perforated the septa, it starts a spindle-shaped carton nest in the bole, a little distance above the ground.

This so-called "metropolitan nest," which was discovered by von Ihering, resembles the carton nests built by other species of the genus on the branches of *Cecropia* and other trees. Where the nest occurs the bole of the *Cecropia* presents a spindle-shaped enlargement, which von Ihering regards as a gall—"the largest known gall," but his figures and several of these nests recently acquired by the American Museum of Natural History prove conclusively that such an interpretation is erroneous. The wall of the hollow trunk where it encloses the nest, shows no structural modification except a bending outward of the woody fibers. About half the thickness of this wall is gnawed away by the ants from the inside, leaving a thin zone encircling the trunk, which naturally bulges out under the weight of the superposed trunk and crown of foliage. As there is no hypertrophy of the tissues in the spindle-shaped deformation, the term gall, as applied to a structure of such simple mechanical origin, is a misnomer. When the metropolitan nest is established the ants make a large entrance in

the adjacent wall of the trunk and through this and the other openings in the branches pass to and from the foliage (Wheeler).

Maregravius in 1648 (p. 91)¹ first mentions the constant occurrence of ants in the cavities of the stem of a *Cecropia*. Belt (1874, p. 222) leads the series of modern writers with his studies of Nicaraguan *Cecropiæ*. In his opinion the ants protect the tree; he found the stems of *Cecropiæ* inhabited by three species of ants and also by coccids attended by these insects. Fritz Müller (1876 and 1880) described the origin of the colonies of *Azteca* in *Cecropia adenopus* in Southern Brazil and called attention to the oval depression or prostoma by which the ants always enter the hollow internodes. He also discovered the food-bodies produced between the hairs of the trichilium at the base of the petiole and saw that the ants carried them off to their abodes. Schimper's (1888) careful investigations brought to light additional facts; he proposed the term "Mullerian bodies" for the food-bodies produced by the trichilium. They are white, pear-shaped or oval bodies composed of cells rich in proteids and fatty oils, so they can not be regarded as excreta. Since they are of no use to the plant save to attract ants, Schimper believes that they were originally mucus- or resin-glands which have become highly modified through adaptation to the ants. A similar adaptation is found, he thinks, in the prostoma and the peculiar structure of the stem at that particular spot where only soft parenchym and mucus-vessels are present. Both F. Müller and Schimper consider the leaf-cutting ants (*Attini*) the chief enemies of the *Cecropia* against which the protection by *Azteca* is devised. These authors call the ant which they observed on *C. adenopus*, "*Azteca instabilis*," but, as shown by Emery, this is *A. muelleri* Emery and not Smith's *A. instabilis*. Later observers, such as Ule (1897, 1905b, 1906b), Rettig (1904), H. v. Ihering (1907), K. Fiebrig (1909), and Wheeler (1908a, 1913), have offered many objections to the Belt-Schimper hypothesis of symbiosis between *Azteca* and *Cecropia adenopus*. Among other points, it is very doubtful whether the leaves of *Cecropia* are particularly attractive to leaf-cutting ants; moreover, the foliage of older trees which are occupied by *Azteca* is often much eaten by sloths, caterpillars, and other insects. Rettig calls attention to the presence on the leaves of *Cecropia adenopus* of bead-like glands containing proteids and fatty oils and which are also collected and used as food by the ants.

H. v. Ihering found *Azteca nigella* Emery nesting in the internodes of younger plants, 2 to 3 m. high, while older plants with a "metropolitan

¹John Ray (1688, p. 1373) reproduces Maregravius' observations

nest" in a spindle-shaped swelling of the bole were inhabited exclusively by *A. muelleri* Emery; he believes that this is a case of dimorphism between the younger and older generations of workers in the same colony. He has, however, not given any conclusive evidence that such is the case, since he has not observed transitional colonies of these two forms.¹ H. v. Ihering also found *A. lanuginosa* Emery in *Cecropia adenopus*; he mentions the frequent occurrence of coccids (*Lachnodiella cecropiæ* H. v. Ihering) in the nests. In his opinion, the main food of the adult ants consists in the soft pith-parenchyma of the upper, still growing internodes, also in the Müllerian bodies. He was unable to find how the larvæ are fed.

Fiebrig's (1909) observations were made in Paraguay on what he calls "*Cecropia peltata* L.," but what is evidently not the Central American *C. peltata* but *C. adenopus* of Brazil.² The internodes were practically always inhabited by *Azteca alfaroi* variety *mixta* Forel. The ants go only short distances from their exit holes, unless disturbed, when they become very aggressive. Fiebrig thinks that the main food of the ants is the Mullerian bodies, on which the larvæ are probably fed exclusively, while the workers may also eat soft pith tissues and feed on the sweet fruits of the tree. There is little doubt that *A. alfaroi* is wholly vegetarian, while most other species of *Azteca* are carnivorous. In Paraguay the internodes of *Cecropia* are very often invaded by caterpillars (*Heliothis* species). The very young larvæ of this moth were repeatedly observed in internodes where a queen ant had just started a new colony; later on the caterpillars crowd the ants out and finally occupy the entire branch and destroy even the septa.

Wheeler has called attention to the occurrence in Cuba and Porto Rico of species of *Cecropia* fully equipped with prostoma and Mullerian bodies, though never tenanted by *Azteca*, since this genus of ants is lacking on all the larger Antilles.

Cecropia lyratiloba Miquel. Under this name a swamp *Cecropia* of southern Brazil was studied by H. v. Ihering (1907). It possesses the same so-called myrmecophilous structures as *C. adenopus* and is also inhabited by a species of *Azteca*.

Cecropia sciadophylla Martius. Brazil. Inhabited by *Azteca emeryi* Forel (Ulc).

¹Emery (1912, 'Gen. Insect., Dolichoderinæ,' p. 34) still regards *nigella* as a distinct variety of *A. muelleri*.

²Chodat and Vischer (1920, p. 235) assert that *A. adenopus* is the only species of the genus found in Paraguay.

Polygonaceæ

A cosmopolitan family of 800 species, belonging to 34 genera. The myrmecophytic forms are trees or bushes of South and Central America.

Triplaris C. A. Meyer. Tropical South and Central America. Represented by ten species, all of which have apparently hollow internodes, but the branches are not inflated, though they are usually inhabited by ants.¹ It has been claimed that in some cases the entrance to the cavity is preformed.

Emery (1894a) described *Pseudomyrma arboris-sanctæ* from Bolivia, in stems of a *Triplaris* (collected by Balzan); Ule found *Pseudomyrma sericca* variety *rubiginosa* Stitz (Stitz, 1913a) inside the stems of an unidentified *Triplaris* of Brazil.

Of his *Pseudomyrma arboris-sanctæ* subspecies *symbiotica*, Forel (1904, pp. 39-40) has this to say:

I discovered this race in March 1896 at Dibulla, at the foot of the Sierra Nevada de Sta-Marta, Columbia, in the following manner. Having laid my hand on the trunk of a young, green tree, about 4 meters high, and with large leaves, I was stung, and discovered on the trunk this *Pseudomyrma*, the cause of the sting. Noting the aggressive behavior of these ants, I suspected a symbiotic relation between the tree and them, for other *Pseudomyrmæ* which run on trees take to flight instead of attacking. Finding, however, no dry branch and no aperture, I was at first puzzled. On noticing some passing Indians, I had the tree cut down with their machetes. I then broke the flexible, fresh branches of the tree and found them all provided with a very narrow pith channel. These channels constituted, from one end to the other of all branches and twigs of the tree, the nest of the *Pseudomyrmæ*, which were occupying them in a file, with their males, their larvæ, and their nymphs, having just room to cross over one another notwithstanding the slenderness of their body. This curious habitation perplexed me much and I was wondering where the female foundress of the formicary might have entered this perfectly green tree, without any dry branch and apparently

¹One of the earliest records of myrmecophytism in *Triplaris* is that by Weddell (1840, pp. 262-263, footnote). This publication not being accessible to many myrmecologists, I have reproduced Weddell's notes below; they contain name and description of an ant which has apparently been overlooked by subsequent authors; the species is evidently a *Pseudomyrma* and perhaps the one known as *P. arboris-sanctæ* Emery.

"Le tronc, les branches et même les plus petits rameaux des espèces de ce genre sont fistuleux et servent d'habitation à une fourmi d'une espèce particulière qui exhale, lorsqu'elle est excitée, une odeur assez agréable, comparable à celle que répandent les Cicindèles. Si l'on vient accidentellement à toucher le tronc d'un *Triplaris* et surtout à lui imprimer un choc, on voit les fourmis surgir par centaines de l'intérieur de l'arbre par de petits canaux qui font communiquer avec l'extérieur son canal médullaire, et, si l'on ne s'éloigne au plus vite, on est bientôt couvert de ces hordes dangereuses dont la morsure est bien plus douloureuse en proportion que les piqures d'aucun autre insecte que je connaisse.

"C'est une chose singulière que, à quelque époque de leur vie que l'on examine les *Triplaris* dans leurs forêts, on soit toujours sûr d'y rencontrer ces fourmis. Il est encore bien curieux que, dans les *Ruprechtia* que quelques auteurs réunissent encore aux *Triplaris*, on n'en trouve jamais.

"Je ne crois pas que cet insecte ait été observé dans d'autres conditions que celles que j'ai notées; sa forme linéaire est particulièrement adaptée à son genre de vie. J'ai eu occasion de l'examiner et même de souffrir ses atteintes dans bien des parties du Brésil, en Bolivie et au Pérou; et partout il m'a paru identique. Déjà plusieurs voyageurs ont signalé une partie des faits dont il vient d'être question, et ils ont rapporté la fourmi du *Triplaris* au genre *Myrmica* de Latreille; mais je ne sache pas qu'en lui ait donné de nom spécifique; on pourrait lui appliquer celui de *Myrmica triplarina*. Elle est ordinairement d'un brun clair. Sa longueur est de 6 ou 7 millimètres, et sa largeur de 1 millimètre; l'abdomen est cylindrique et un peu atténué vers son extrémité postérieure qui est poilue."

without any exit hole. After long, unsuccessful investigation of all the branches, I inspected the lower portion of the trunk and finally discovered there the remains of an early branchlet, dried and broken off, but with a pith cavity communicating with the central cavity of the very trunk. It is by this old branch that the *Pseudomyrma* came and went.

Warming (1894) has published some interesting information on a *Triplaris* of Venezuela, which he doubtfully identifies as *T. americana*. The ants found in this plant belonged to a species of *Pseudomyrma* which he calls "*P. mordax* Meinert," a name not backed by any description in the literature.

T. americana Linnæus. South America. The earliest accurate account of myrmecophilism in the genus *Triplaris* was published, it appears, by Robert Schomburgk (1838, pp. 264-267) for the species under discussion. After a description of this tree, which he found common on the sandy banks of the inland rivers in Guiana, and often overtopping the other vegetation, he continues:

The incautious botanist, who, allured by the deceptive appearance, should approach the tree to pluck the blossoms, would bitterly rue his attempt. The trunk and branches of the tree are hollow, like those of the trumpet tree (*Cecropia*), and provided with partitions, which answer to the position of the leaves on the outside. These hollows are inhabited by a light brownish ant, about two- to three-tenths of an inch long, which inflicts the most painful bites. Its antennæ are placed near the middle of the anterior portion of the head; mandibles triangular; peduncle of the abdomen with two rings; the anus hairy and provided with a sting or piercer. They fall upon their prey with the greatest virulence, and insert their mandibles almost instantly, as soon as they come in contact with any soft substance, emitting a whitish fluid; their bite causes swelling and itching for several days. If they find themselves captured, they attack and kill one another like the scorpions. The Arawak Indians call the tree Jacuna, and the ant Jacuna sac; the Warrows Epouahari, the literal translation being ant tree; the Caribis Itassi; the colonists, from its growth, "lon John."

Richard Schomburgk (1848, II, pp. 449-450) also records his painful experience with the same tree, which he found growing on the banks of the Barima and Barama Rivers, British Guiana.

Penzig found the caulinary cavities of *T. americana*, cultivated at Buitenzorg, Java, occupied by *Dolichoderus bituberculatus* (Mortco, 1904).

T. Cumingiana Fischer and Meyer. Central America. Wheeler (1913) observed this species in Panama and writes about it as follows:

These trees were 15 to 20 ft. high, with very slender trunk, smooth, light gray bark, and long, narrow, lanceolate leaves. When the trunk was cut down and split longitudinally, it was seen to have a very slender cavity in the centre and extending its full length, and communicating with a similar slender cavity in the centre of each branch. This continuous system of cavities communicated with the surface by numerous slender galleries, excavated by the ants, and terminating in small round orifices, which served as exits and entrances.

Each tree was occupied by a single large colony of *Pseudomyrma arboris-sanctæ* Emery. Wheeler adds: "as the *Triplaris* trees were isolated and as their bases must stand in the water during the rainy season, it is difficult to understand how the ants manage to exist, unless they remain rather dormant this season or find some hitherto unknown food supply on the foliage." Recent, unpublished observations of Prof. I. W. Bailey on *T. surinamensis*, in British Guiana, however, show that the cavities of *Triplaris* contain great numbers of coccids from which the *Pseudomyrmæ* obtain at least much of their food.

T. caracasana Chamisso and Schlechtendal. Venezuela. Trunk inhabited by ants (Karsten in Huth, 1887). Schimper (1888) examined branches sent to him by Ernst and curiously enough states that they presented no adaptations to ants: "the branches possess an inner cavity which is only 5-8 mm. wide and interrupted by diaphragms; round apertures, pierced by the ants, lead into the cavity." He does not believe that there is any true symbiosis in this case.

T. nolitangere Weddell. Brazil. Stem inhabited by ants (Huth, 1887).

T. surinamensis Chamisso and Schlechtendal. Brazil, Guiana. Myrmecophytic (Spruce, 1908).

T. Macombii Don. Smith. Guatemala. Wheeler (1913) says:

This is a larger tree (than *T. Cumingiana*), often attaining a height of 30 to 40 ft., with more diffuse branches and large, coarse, ovate leaves. Early in January it began to put forth bunches of long, yellowish flower-spikes, which were covered with a deciduous sheath. The branches have much larger cavities than in *T. Cumingiana* and the septa at the nodes are not broken through. On examining the surfaces of the branches, each internode is seen to be surrounded near its distal end by a circle of lenticels, and one of these, for some unknown reason, often becomes considerably enlarged and bears a long slit-shaped impression. It is in this impression that the queen ant makes the circular perforation that permits her to enter and take possession of the internodal cavity.

The same observer found the cavities of this species occupied by several species of ants belonging to the genera *Crematogaster*, *Pheidole*, *Tapinoma*, and *Iridomyrmex*, but two species were especially common, a small, black, narrow-headed *Azteca* and the black *Pseudomyrma sericea* Mayr. None of these, however, are obligatory plant ants.

T. Schomburgkiana Benth. Brazil. Inhabited by ants (Spruce, 1908). Ule (1917) found in this species *Pseudomyrma dendroica* Forel and *P. triplaris* Forel.

Pseudomyrma dendroica was originally described from specimens found by A. Gældi in the pith channel of young, unidentified *Triplaris* on the Rio Purus, Brazil. Some of these plants having been introduced

into the Botanical Garden at Pará, Gældi observed that this ant soon invaded one the *Triplaris* of the Garden which thus far had not been inhabited (Forel, 1904, p. 41).

Ruprechtia C. A. Meyer. Tropical and subtropical South America. There are twenty species, most of which are said to possess solid branches; the following is perhaps an exception.

R. Jamesoni Meisner. Brazil. The stem and branches are hollow and inhabited by ants (Spruce, 1908).

Symmeria Benth. This genus contains two species; one has been described from Senegambia; the other, *S. paniculata* Benth., according to Spruce (1908), is an ant plant; it occurs in Guiana, northern Brazil, and curiously enough also in Sierra Leone.

Coccoloba Jacquin (including *Campderia* Benth.). Tropical and subtropical America. A large genus, with about 125 species; only one of them has been mentioned as a myrmecophyte, but the others should also be studied in this respect. The common sea-side grape, *Coccoloba uvifera* Linnæus, in Porto Rico, sometimes has ants nesting in some of the internodes; but these are facultative forms, such as *Camponotus sexguttatus* (Fabricius), more common elsewhere. This species, at least, cannot be regarded as a myrmecophyte (Wheeler, 1908a, p. 157).

C. parimensis Benth. British Guiana, Brazil. The stem and branches are hollow, but not inflated, and are inhabited by ants (Spruce, 1908).

Myristicaceæ

A small, exclusively tropical family, which, according to Warburg's monograph (1897), contains 15 genera with about 240 species.

Myristica Linnæus. Indomalayan Region; eighty species. In two related species from New Guinea, the internodes are in places swollen and hollow; these swellings are irregularly scattered along the branches, and their inner cavities do not communicate with one another; they are inhabited by ants, which pierce the entrances, often slit-like and placed on the side facing the leaf of the lower node. Warburg (1897), who has studied their histology, concludes that these swellings are probably not hereditary, but produced by the irritation of the ants; he considers them true ant galls, not myrmecodomatia. There is, however, no experimental proof that ants can produce such swellings.

M. subalulata Miquel (= *M. myrmecophila* Beccari). This species has been studied by Beccari (1884) and Warburg (1892; 1897); the latter figures (1897, Pl. xi) coccids on the inner walls of the swellings.

M. heterophylla K. Schumann. Swellings on the branches inhabited by ants (Schumann, 1890; Warburg, 1897).

M. curyocarpa Warburg, of New Guinea, is perhaps also inhabited by ants.

It is still somewhat doubtful whether these *Myristicæ* are true myrmecophytes.

Monimiaceæ

Tropical regions of both hemispheres. Represented by 250 species, belonging to 30 genera.

Kibara Endlicher. Eastern India, Malay Archipelago. With about 14 species.

K. formicarum Beccari. New Guinea. The branches are hollow and swollen at the internodes just beneath the insertion of the leaves; ants live inside together with coccids (Beccari, 1877, 'Malesia,' I, pt. 2, pp. 189-192).

Anthobembix Perkins. New Guinea. Contains two species, one of which is a myrmecophyte.

A. hospitans (Beccari) (= *Kibara hospitans* Beccari). Branches club-shaped below the nodes; these swellings hollow, pierced with apertures and inhabited by ants (*Iridomyrmex scrutator* Smith) together with coccids (*Myzolecanium kibaræ* Targioni) (Beccari, 1877, *loc. cit.*).

Lauraceæ

Tropical and subtropical regions of both hemispheres. Includes 1100 species, belonging to 48 genera.

Pleurothyrium Nees. Brazil, Peru. There are five species, of which the following three have swollen, fistulose branches and probably are myrmecophytes (Mez, 1888 and 1889; K. Schumann, 1888).

P. cuneifolium Nees. Peru, Brazil. Pæppig has mentioned the occurrence of ants on this plant: "in ramulis revera fistulosis degunt fornicarum agnina pessime pungentia." Slits, 1 to 2 mm. wide, serve as entrances to the cavities (Mez, 1889, p. 471).

P. Pæppigii Nees. Peru.

P. chrysophyllum Nees. Peru.

Ocotea Aublet. Tropics of both hemispheres. About 200 species, some of which have pouches or bullæ, more or less pronounced, placed in the axils of the side-veins and projecting towards the upper side of the leaf; such species are *O. phillyræoides* (Nees) of Brazil, *O. Mandonii* Mez of Bolivia, *O. Bernouilliana* Mez of Guatemala, and *O. bullata* E. Meyer of the coastal region of Cape Colony and Natal. In the last-named

species the pouches are large pits with ciliolate orifices on the under side in the axils of the lowest one or two pairs of nerves, the pits corresponding to large hollow tubercles on the upper side. Whether these pouches are merely acarodomatia or occasionally settled by ants is not known.

Nepenthaceæ

Oriental Region, the Seychelles, and Madagascar. Only one genus, *Nepenthes* Linnæus, with some 60 species, one of which has been recorded as myrmecophytic, but the case needs further investigation.

N. bicalcarata Hooker fil. Borneo. The petiole of the pitcher-shaped leaves is curled up and, in the curled part, swollen and hollow. According to Shelford (1916), there is no evidence that this cavity is inhabited by ants; while Beccari (1884) saw an opening leading inside and apparently found ants in the swelling.

Rosaceæ

Cosmopolitan. Includes 1700 species, belonging to 102 genera.

Hirtella Linnæus. Tropical America, with forty species; one species occurs in Madagascar. Myrmecophytism seems to be exceptional in this genus, as is also the case in *Cola* and *Randia*.

H. physophora Martius. The cordate leaves have at the base of the blade a pair of compresso-globose sacs inhabited by ants (Spruce, 1908).

Leguminosæ

Cosmopolitan, with 12,000 species and 530 genera. This and the Compositæ are the largest families of plants.

Acacia Willdenow. Tropical and subtropical regions of both hemispheres. There are over 600 species.

The so-called bull's-horn acacias of Mexico, Central America, and Cuba are apparently true myrmecophytes; their stipular thorns are much enlarged and flattened or inflated; they are usually hollowed out by ants, which pierce an entrance below the tip of the thorn, more rarely near its base, and establish their nests inside; furthermore, the young leaves bear at the tips of their pinnæ, minute, bright yellow food-bodies (Beltian bodies)¹ which are eagerly collected by the ants and carried inside the thorns. These plants all grow in dry or semi-desert regions under conditions very different from those of other myrmecophytes.

¹Meneghini and Savi (1844), Fr. Darwin (1877), and A. F. W. Schimper (1888), who have studied the inner structure and development of these Beltian bodies, all agree that they are homologues of the glandular serrations which frequently occur on the margins of young leaves. Such glands often secrete mucus or resin and, as a rule, disappear at an early stage; while in the ant acacias they increase considerably, are filled with proteins and fats and, when not removed by the ants, finally drop off.

One of the Mexican species was figured and described by Francisco Hernandez in 1651 (p. 86, Cap. LIII) as *Arbor cornigera* or the Huitz-mamaxalli ("forked-thorn") of the Aztecs. In accordance with the ideas of his time, Hernandez believed that the thorns themselves generated the ants: "generantur præterea intra corniculas fornicæ quædam tenues fulvæque et nigricantes." Linnaeus' *Acacia cornigera*, however, is an altogether different plant and was described from a cultivated specimen growing in the garden of George Clifford, between Haarlem and Leyden, Holland; its origin is unknown. In fact, until quite recently, such confusion existed in the classification of bull's-horn acacias that it is almost impossible to recognize the species on which ecological observations have been published by Belt (1874), Beccari (1884), Wheeler (1913), Wasmann (1915a), and others.

H. Schenek (1913, 1914) and W. E. Safford (1910, 1914, 1915) have shown that the bull's-horn acacias contain a number of more or less related forms which are probably only partly known; twenty-seven species have thus far been described. It must be expected that these numerous allied forms, which often differ markedly in size and shape of their thorns, will be found to harbor a corresponding variety of guest ants. Owing to the uncertainty of identification of the plants studied by various authors, the following list of ants will merely give a general hint as to the species which may be expected in these plants.

It may be of interest to note that some bull's-horn acacias have been cultivated in hothouses in Europe (Commelin; Linnaeus; Beccari) and in certain botanical gardens of the tropics (in Java, Raciborski; in Ceylon, Ridley; in Gaboon and Cameroon, H. Schenek; also in Cuba, according to Wheeler). The thorns are then swollen and hollow, as on the wild-growing plants, but are not attacked by ants.¹ Raciborski (1900) remarks that the food-bodies of such acacias are not collected by the ants in Java and that this is true also for the Mullerian bodies of the *Cecropiæ* which he saw cultivated at Buitenzorg.

Belt (1874), in Nicaragua, found in the thorns of his "*Acacia cornigera*" specimens of *Pseudomyrma gracilis* (Fabricius), = *P. bicolor* Smith, and more rarely of a *Crematogaster*. Emery (1890 and 1891) has given a long list of ants found by Alfaro in the thorns of unidentified Costa Rican acacias; only three of these, however, *Pseudomyrma betti* Emery,

¹Dr. W. E. Safford kindly informs me that a number of bull's-horn acacias are now being cultivated in a greenhouse in Washington, D. C. In each case the swollen thorns have maintained their characteristic shape, in spite of the absence of ants. Prof. Wheeler saw two Central American bull's-horn acacias growing in the Botanical Garden of Port of Spain, Trinidad. All their thorns were inhabited by a native, black *Crematogaster* which had even enveloped some of the thorns with carton. The ants were extremely numerous and vicious.

P. spinicola Emery, and *P. nigrocincta* Emery, he considers obligatory acacia ants¹: "these species occur only on acacias, while other species of the same genus burrow their nests in wood; all three pierce the thorns close to the tip, when they are still young and soft, as Belt describes it; never was more than one of these three species found on a single tree and in each case the ant inhabited all the thorns on the living branches of the acacia." When the branches die, these *Pseudomyrmæ* leave the thorns, which are then occupied by many other ants: *Pseudomyrma gracilis* variety *mexicana* Roger, *P. subtilissima* Emery, *P. nigropilosa* Emery, *P. kunckeli* Emery, *Crematogaster brevispinosa* Mayr, *Cryptocerus minutus* (Fabricius), *Camponotus rectangularis* Emery, and others; some of these species may occasionally invade young thorns of living branches, but, as they often occur elsewhere, they must be designated as facultative guests of the plant.

Wheeler (1913) found *Pseudomyrma spinicola* Emery on "*Acacia sphærocephala*" in Panama, and *P. belti* Emery with its subspecies *fulvescens* Emery on "*A. cornigera*" and "*A. Hindsii*" in Guatemala. Dr. P. P. Calvert, moreover, sent him *P. belti* and *P. nigrocincta* taken from acacia thorns in Costa Rica. Wheeler agrees with Emery that these four forms are, so far as known, the only obligatory acacia ants of Central America; among the facultative acacia ants he mentions *Camponotus planatus* Roger, *Pseudomyrma gracilis* (Fabricius), and *Solenopsis* species, taken by him in Guatemala; also *Pseudomyrma nigropilosa* Emery found by Calvert in Costa Rica.

Wasmann (1915a) described *Pseudomyrma wasmanni* Wheeler, = *P. canescens* Wasmann, nec Smith, from the swollen thorns of "*Acacia sphærocephala*" collected at Tampico, Mexico.

South American ant acacias are thus far known from Paraguay only. J. Bohls collected there in woody, expanded thorns of an unidentified acacia eleven species of ants: *Pseudomyrma acanthobia* Emery and variety *fuscata* Emery, *Cryptocerus pilosus* Emery, *C. bohlsi* Emery, *C. peltatus* Emery, *C. quadratus* Mayr, *C. pallens* Klug, *C. pusillus* Klug, *C. grandinosus* F. Smith, *Crematogaster brevispinosa* Mayr, and *Myrmelachista nodifera* variety *flavicornis* Emery. In his report of this collection Emery (1896a) remarks: "I have found most of the thorns (sent by Bohls) which still contained ants, inhabited by *Pseudomyrma*, which had its narrow galleries burrowed in the wood. The large *Cryptocerus* had completely hollowed out the thorns occupied by them. The openings

¹The terms "obligatory" and "facultative" as applied to acacia ants were proposed by Wheeler (1913).

of the *Pseudomyrma* nests were placed not far from the tip, those of the other species pierced at various levels, often also several on one thorn." The only other observations on these interesting plants were made by Fiebrig (1909), who studied *Acacia cavenia* Hooker and Arnott in the Chaco of northern Paraguay; the thorns of this species are very large, 90 mm. long and 8 mm. wide, and usually inhabited by *Pseudomyrma fiebrigi* Forel; normal thorns are filled with pith; in those occupied by ants that substance is more or less removed and an opening is found below the tip. Frequently, however, the pith is destroyed by a caterpillar which pupates inside, the moth escaping through a hole near the point of the thorn. Fiebrig believes that the ants appropriate these excavated thorns, using apertures made by the moth. According to Chodat and Carisso (1920), the swelling of the thorns of *A. cavenia* is due to the sting of an insect, the gall thus produced being eventually settled by ants, after its maker has left it. I cannot agree with this explanation.

In a foregoing chapter (p. 372) I have discussed the so-called ant acacias of East and South Africa and have given my reason for not regarding them as true myrmecophytes. In their case, the swellings of the thorns are typical insect galls, probably produced by a lepidopterous larva. When the gall maker has left, the empty shelters may be invaded by various ants, even before they are completely dry, thus simulating myrmecodomatia.

Sclerolobium Vogel. Tropical South America. Containing twelve species.

Only one of the species, *S. odoratissimum* Spruce, of Brazil (Rio Negro), is said to be myrmecophilous; its leaves have a large sac, furrowed along the upper face and extending upward from the knee of the petiole to the base of the second pair of leaflets (Spruce, 1908). It is possible that this pouch is merely an insect gall which, when empty, becomes settled by ants.

Humboldtia Vahl (= *Batschia* Vahl). Ceylon and British India. Represented by four species, one of which is myrmecophilous.

H. laurifolia Vahl. India. The swollen internodes are occupied by ants (Bower, 1886 and 1887; Schimper, 1903; Morteo, 1904; Ridley, 1910). Figured by Taubert, 1894, in Engler and Prantl, 'Die Natürl. Pflanzenfam.,' III, pt. 3, p. 143, fig. 80, and by A. F. W. Schimper, 1903, 'Plant Geography,' p. 147, fig. 83; this figure is also copied by Escherich (1906b) and Wheeler (1910b).

Escherich (1911a, pp. 46-47) re-examined *H. laurifolia* in the Botanical Garden at Peradeniya, Ceylon. He found that only compara-

tively few of the swollen internodes (at most 20 per cent in the Garden, as contrasted with 50 per cent in the wild state, according to Green) contained a number of species of ants that are also found nesting in other locations (*Technomyrmex*, *Tapinoma*, *Monomorium*, *Crematogaster*, etc.). Since the ants are not in the least aggressive and, furthermore, often keep coccids inside the domatia, he concludes that they are decidedly noxious to the plant, the more so since they frequently attract woodpeckers which damage the branches in order to feed on them and their brood.

Schotia Jacquin (= *Theodora* Medikus). Tropical Africa. There are twelve species, one of them possibly myrmecophytic.

S. africana (Baillon) (= *S. humboldtioides* Oliver). Cameroon, Spanish Guinea, Gaboon. The young branches often have swollen and hollow internodes settled by ants. There is still a possibility that these enlargements are mere insect galls, which are invaded by ants after being left by their makers (see above, p. 409).

Tachigalia Aublet (= *Cubza* Schreber; *Tachia* Persoon). South America. Includes six species, all of which have inflated petioles inhabited by ants. *Pseudomyrma picta* Stitz and *Azteca brevicornis* (Mayr) were found in *Tachigalia* by Ule in Brazil (Stitz, 1913a).

T. caripes Spruce. Brazil. The trigonous petioles are mostly dilated at the base into a fusiform sac tenanted by ants (Spruce, 1908).

T. ptychophysca Spruce. Brazil. Like the preceding (Spruce, 1908).

T. formicarum Harms. Eastern Peru. The petiole is swollen and inhabited by *Pseudomyrma* (Ule, 1908).

Platymiscium Vogel. South America. Contains fifteen species.

The stem is hollowed and inhabited by ants, and even sometimes dilated at the nodes (Spruce, 1908).

Meliaceæ

Tropical and subtropical regions of the globe. Has 42 genera, with about 700 species.

Chisocheton Blume. Indomalayan Region. About thirty species.

C. pachyrhachis Harms. New Guinea. A tree with the nodes of the branches and the base of the petiole swollen and hollow; several apertures leading into the cavity (K. Schumann and K. Lauterbach, 1901, p. 382).

Aphanamixis Blume. Indomalayan Region. Includes eleven species.

A. myrmecophila (Warburg) (= *Amoora myrmecophila* Warburg). New Guinea. The branches are often swollen and excavated, even the younger upper portions, the growing extremity narrowing very abruptly;

several apertures lead inside the irregular cavities, which have smooth, brown walls; the swellings are inhabited by ants (Warburg, 1894, pp. 194-196).

Euphorbiaceæ

A large, cosmopolitan family, with 4500 species, belonging to about 250 genera.

Endospermum Bentham. Indomalayan Region to New Guinea. Includes twelve species, two of which are to all appearances true myrmecophytes.

E. moluccanum (Teysmann and Binnendijk). Amboina, Moluccas, Celebes. There is a question whether this species is myrmecophytic. According to Beccari, this is the plant figured by Rumphius (1741, II, pp. 257-259, Pl. I.XXXV) as "*Arbor Regis*".¹ In the latter's description, however, a confusion may have been made between several plants; so that it is by no means sure that the following remarks concerning the myrmecodomatia of his *Arbor Regis* apply to *E. moluccanum*:

Truncus, omnesque crassi rami nullo constant corde, sed excavati sunt, ejusque loco referti sunt plurimis magnis et nigricantibus formicis, quæ in una alterave parte truncum perforant, et fenestras quasi formant, perambulantes illum usque ad ramorum extremum tanquam murum concavum, ita ut hæc arbor solo ex cortice suum hauriat nutrimentum, tenuiores vero rami medullam gerunt, qualem *Sambucus* habet. Si quidam amputetur ramus, formicæ hæc magna vi ac celeritate excurrunt, mox circumstantes invadentes homines ac mordentes tanto impetu, ut periculosum valde sit huic accedere arbori, immo totum circa hanc solum mordentibus hisce animalibus repletur, quæ adpropinquantium etiam pedes infestant. Observavi autem Indos non ita horum morsus presentire per duram ipsorum cutim, ac nos, unde et intrepide ad illam accedunt arborem.

The relations of *E. moluccanum* to ants have apparently not been studied in the field since Rumphius' time.

E. formicarum Beccari. New Guinea, Bismarek Archipelago. In New Guinea, according to Beccari (1884), the branches are normally swollen and hollow toward their extremity; he found them inhabited by *Camponotus angulatus* Smith, which had apparently pierced the entrances to the cavities. Dahl (1901) describes this plant in the Bismarek Archipelago as having normal branches, filled with pith which is partly excavated by ants, *Camponotus (Colobopsis) quadriceps* (Smith).

Macaranga DuPetit-Thouars. Tropical and subtropical regions of the Old World. About 170 species, a number of which are myrmecophytic.

¹Merrill (1917) admits the correctness of Beccari's reduction of Rumphius' "*Arbor Regis*" to *E. moluccanum*.

Donisthorpe (1917) described *Dolichodcrus (Hypoclinea) crawleyi* from Singapore, "associated with species of *Lecanium* (coccids) in hollow stems of *Macaranga*." Wheeler (1919, p. 77) also mentions *Crematogaster (Decacrema) decamera* (Forel) "from *Macaranga* with slightly trifid leaves" at Kuching, Borneo.

M. hypoleuca (Reichenbach fil. and Zollinger). Malay Peninsula, Sumatra, Borneo. Inhabited by forms of *Crematogaster (Decacrema) borneensis* (Ern. André) (Viehmeier, 1916).

M. caladifolia Beccari. Borneo (Beccari, 1884).

M. formicarum Pax and O. Hoffmann. Borneo. A low tree with thick, hollow branches which are pierced with an entrance and inhabited by ants (Pax, 1914).

In these three species ants live within the hollow, slightly swollen stem and branches, and also underneath the lanceolate, erect, persistent bud-bracts in the axils of the leaves; food-bodies, white and globular, are scattered on the back of the young leaves between the raised veins. The food globules are most plentiful in plants not settled by ants, and have been seen carried about between the mandibles of these insects (Beccari, 1884; Ridley, 1910; Pax, 1914; Shelford, 1916).

M. triloba (Reinwardt). Malay Peninsula and Archipelago.

M. Griffithiana Mueller. Malay Peninsula.

M. Hulletii King. Malay Peninsula.

In these three species, the stems are also hollow and settled by ants; furthermore, the bud-bracts are reflexed into a ring-like pouch which almost completely surrounds the stem. The concave under side of the bracts bears abundant pear-shaped or globular, white food-bodies, which are much sought for by the ants and are conveyed to the nest in the hollow stem, where the larvæ are fed on them; the ants not only hide beneath the bracts but occasionally take their larvæ there. *M. Hosei* King possibly has similar myrmecodomatia. The ant of *M. triloba* is a *Crematogaster* near *C. daisyi* (Forel) (W. Smith, 1903; Ridley, 1910).

In an unidentified species of *Macaranga* of Sarawak, the bracts are very large, lanceolate, acuminate, deflexed, coriaceous, not appressed to the stem, but concave, thus providing a nidus or feeding ground for ants (Ridley, 1910).

M. saccifera Pax.

M. Schweinfurthii Pax (= *M. rosea* Pax).

The above two species are from Tropical Africa and have pouch-like stipules, which in *M. saccifera* are sometimes inhabited by ants of the genus *Crematogaster* (see above, p. 412).

Mabea Aublet. South America. Contains thirty species, some of which have long, hollow branches, often settled by ants (Spruce, 1908).

Sterculiaceæ

Tropical regions of both hemispheres. Represented by 820 species and 57 genera.

Cola Schott and Endlicher. Tropical Africa. With forty-five species. The following three closely allied forms have at the base of the leaf-blade a pair of pouches which are often inhabited by small species of *Engramma* (see above, p. 417).

C. Deweveri de Wildeman and Durand.

C. Laurentii De Wildeman.

C. marsupium K. Schumann.

Scaphopetalum Masters. Tropical Africa. Includes eight species, two of which have an elongate pouch at the base of the leaf-blade often occupied by ants of the genus *Engramma* (see above, p. 422).

S. Deweveri De Wildeman and Durand. Belgian Congo.

S. Thonneri De Wildeman and Durand. Belgian Congo, Cameroon.

Flacourtiaceæ

Tropical regions of both hemispheres. With 650 species and 84 genera.

Barteria J. D. Hooker. Tropical Africa. Includes four species, all of which probably have hollow or swollen internodes, normally inhabited by *Pachysima æthiops* (F. Smith) or *P. latifrons* (Emery); accidentally by other ants (see above p. 432).

B. Deweveri De Wildeman and Durand. Belgian Congo.

B. fistulosa Masters. Fernando Po, Cameroon, Belgian Congo.

B. nigrilana J. D. Hooker. Southern Nigeria, Cameroon, Spanish Guinea, Gaboon, (Belgian Congo?).

B. Stuhlmannii Engler and Gilg. German East Africa.

Gertrudia K. Schumann. New Guinea. With one species, *G. amplifolia* K. Schumann. It is a tree or shrub with branches "strongly swollen at the apex below the leaf-bud, hollow and with an aperture leading into the cavity (probably a myrmecodomatium)" (K. Schumann and K. Lauterbach, 1901, p. 455, Pl. xv). Perhaps this swelling is only an insect gall.

Melastomataceæ

Tropical and subtropical parts of both hemispheres; very abundant in America, where a few forms reach the Nearetic Region. Represented by 2800 species and 170 genera. With the exception of *Pachycentria*,

which is a doubtful myrmecophyte, all the myrmecophytic members of this family are restricted to the Neotropical Region.

Tococa Martius. South America. Includes forty species which, with one or two exceptions, have ant-pouches on the leaves. Either all the leaves or only one of each pair have a hollow sac or pair of sacs at the base of the blade, or in the upper part of the petiole; these pouches are usually inhabited by ants (species of *Azteca*¹).

T. disolenia Spruce. Brazil (Spruce, 1908).

T. bullifera Spruce. Brazil (Spruce, 1908).

T. macrophysca Spruce. Brazil (Spruce, 1908).

T. formicaria Martius. Brazil (Spix and Martius, 1831).

T. guianensis Aublet. Guiana. Aublet (1775) describes the two pouches which in this species are placed along the upper part of the petiole, each with an opening beneath the base of the leaf-blade; ants are usually found in them and from the description it would seem that they also inhabit the stem of the plant.

Microphysca Naudin. Northern Brazil and Peru. Contains two species, *M. quadrialata* Naudin and *M. rotundifolia* (Spruce), with pouches on the leaves.

Myrmidone Martius. South America. There are two species, both with sacs on the leaves shaped much as in certain forms of *Tococa*.

M. macrosperma Martius. Brazil (Spruce, 1908).

M. rotundifolia Spruce. Brazil (Spruce, 1908).

Maleta Aublet (including *Calophysca* de Candolle). South America. Includes eight species, probably all with ascidia serving as abodes for ants.

M. guianensis Aublet (= *M. hypophysca* Martius). Guiana, Brazil. The branches are fistulose and swollen at the nodes; the leaves also bear pouches (Spruce, 1908).

To judge from his figure, this is the unidentified melastomataceous plant alluded to by Belt (1874, pp. 223-224) in the following passage:

In each leaf, at the base of the laminæ, the petiole or stalk is furnished with a couple of pouches, divided from each other by the midrib, as shown in the figure. Into each of these pouches there is an entrance from the lower side of the leaf. I noticed them first in Northern Brazil, in the province of Maranhão; and afterwards at Pará. Every pouch was occupied by a nest of small black ants; and if the leaf was shaken ever so little, they would rush out and scour all over it in search of the aggressor. I must have tested some hundreds of leaves, and never shook one without the ants coming out, excepting one sickly-looking plant at Pará. In many of the

¹*Azteca trailli* Emery was found in the ascidia of a melastomataceous plant by Schulz at Pará.

pouches I noticed the eggs and young ants, and in some I saw a few dark-colored coccidae or aphides.

M. tococoidea (de Candolle). Brazil, Peru, Guatemala. A large bifid sac at the base of the petiole (Spruce, 1908).

Pachycentria Blume. Malay Archipelago. Includes twelve species. These are woody epiphytes, some of which have tuberous swellings on the roots, filled with a spongy tissue. Ridley did not find any ants inside these enlargements and doubts whether the plants are true myrmecophytes. It is probable that the swellings are merely tubers.

P. macrorhiza Beccari. Borneo. Tuberous and galleried roots inhabited by ants (Shelford, 1916).

P. microstyla Beccari. Borneo. Like the preceding (Shelford, 1916).

Medinilla Gaudichaud. India, Malay Archipelago, Oceania, Madagascar, tropical Africa. Contains over 100 species.

M. loheri Merrill. Luzon, Philippine Islands. Only one of the leaves in each pair is normal; the other is modified into a crop-shaped ascidium opening on the upper side with a slit. According to Loner's observations, this pouch is sometimes occupied by ants, the species of which is not stated (Solereeder, 1920).

M. disparifolia C. B. Robinson. Luzon, Philippine Islands. The leaves have a similar structure as in the foregoing, and are perhaps also used by ants.

Loganiaceæ

Tropical regions of both hemispheres. Represented by 400 species and 35 genera.

Fagraea Thunberg. Oriental Region. Contains twenty-five species. In the three forms enumerated below, the base of the petiole bears auriculate appendages, which are curved downward and more or less pressed against the stem. The cavities thus formed are occupied by ants, which cover the opening with a papery substance and keep their brood inside (Burek, 1891).

F. borneensis Scheffer. Borneo.

F. imperialis Miquel. Sumatra.

F. auriculata Jack. Oriental Region.

Gentianaceæ

Cosmopolitan. Represented by 71 genera, with 900 species.

Tachia Aublet (= *Myrmecia* Schreber). South America. There are four species. Bushes or small trees. The stem and the long, slender

branches are hollow. In the original description of *T. guianensis* Aublet, of Guiana, there is a note as follows: "Le tronc et les branches qui sont creux, servent de retraite aux fourmis; c'est pour cette raison que cet arbrisseau est nommé 'Tachi' par les Galibis, ce qui en leur langue signifie, suivant leur rapport, 'nid de fourmis'" (Huth, 1887; Spruce, 1908).

Apocynaceæ

Cosmopolitan, though chiefly in tropical regions. Represented by 165 genera containing 1300 species.

Epitaberna K. Schumann. One species, *E. myrmacia* K. Schumann, in Cameroon: upper part of the internodes swollen, spindle-shaped, with a cavity inhabited by ants (see above p. 442).

Asclepiadaceæ

Cosmopolitan; chiefly in tropical and subtropical regions, and abundant in Africa. Represented by 267 genera, with 2200 species.

Dischidia R. Brown (including *Conchophyllum* Blume). Oriental Region. Includes fifty species. They are all twining epiphytes; a few are associated with ants.

D. Rafflesiana Wallich. Malay Region.

D. timorensis Decne. Malay Region.

In these two species a certain number of leaves are converted into cone- or pitcher-shaped pouches with an opening at the base through which roots project into the cavity; this pouch also contains soil and sometimes ants, which make regular nests there, with brood (Treub, 1883a; Beccari, 1884; Groom, 1893; Ridley, 1910). The seeds are scattered by ants (see above, p. 357). Beccari found *D. Rafflesiana* in Java inhabited by *Dolichoderus bituberculatus* Mayr and *Crematogaster brevis* Emery.

D. complex Griffith. Malacca (Pearson, 1902).

D. pectenoides Pearson. Philippines (Pearson, 1902).

D. Shelfordii Pearson. Borneo (Pearson, 1903; Shelford, 1916).

In the above three species a certain number of leaves are double pitchers; a small pitcher is found inside each large pitcher; the inner surface of the former is thickly beset with glandular hairs; the larger, outer pitcher is filled with soil and numbers of rootlets, which spring from the petiole or stem and grow through the orifice; in the outer one are found also numbers of ants, *Crematogaster difformis* F. Smith. "Microscopic examination of the inner surface of the outer pitcher revealed the presence of a dense waft of superficial mycelium which was

easily removed on the point of a needle. The growth of this mycelium appeared to be radial, starting from the center of a curious rosette-like structure, formed by shorter hyphæ of a peculiar character. These bore a profuse crop of minute abstricted gemmæ. At the center of each rosette the tissue of the pitcher-wall appeared to have been punctured" (Pearson, 1902, p. 387).

The following three species are doubtful myrmecophytes: *D. Merguensis* Beccari, of Tenasserim; *D. clavata* Wallich, of India; and *D. digitiformis* Beccari, of Celebes.

Borraginaceæ

Cosmopolitan. About 100 genera, with some 1600 species.

Cordia Linnæus. Tropical regions of both hemispheres. Contains 250 species. A few of the South American forms are apparently true myrmecophytes. Ue collected *Cryptocerus cordix* Stitz from an unidentified *Cordia* in Brazil (Stitz, 1913a) and *Azteca longiceps* Emery subspecies *cordicola* Forel was taken from the swellings of a Bolivian species (Forel, 1920a). Chodat and Carisso (1920) regard the caulinary swellings of the species of *Cordia* examined by them in Paraguay, as mere insect galls, subsequently occupied by ants. It can hardly be doubted, however, that they are true myrmecodomatia.

C. Gerascanthos Jacquin. Central and South America. Beccari (1884) noticed on herbarium specimens from Mexico, below the terminal verticil of branches, an obovate, hollow swelling of the stem with a lateral aperture; there were coccids, but no ants inside. Spruce (1908) found these swellings inhabited by ants; and Emery (1890) records *Pseudomyrma belti* subspecies *fulvescens* Emery from this plant in Guatemala; while *Azteca pittieri* Forel variety *emarginatisquamis* Forel occurred in specimens from Costa Rica (Forel, 1920a).

C. nodosa Lamarck. Brazil. Beccari (1884) and Spruce (1908) mention that the stems are swollen and hollow beneath the nodes and settled by ants. Schimper (1888) has studied the myrmecodomatia of this species near Pernambuco: below the false verticil of leaves, side twigs, and inflorescences which terminates the main branches, one frequently finds an elongate, pouch-like swelling which opens above by a small natural aperture placed between the leaves and branches of the false verticil. These pouches are often inhabited by small ants and in such cases their inner wall is covered with a dark brown, earthy crust evidently produced by the ants.¹ See also Rettig (1904). *Azteca stanleyuli* Forel and *A. olitrix* Forel were taken from swellings of *C. nodosa* collected near Para, Brazil (Forel, 1920a).

¹It may be supposed that this dirty layer contains a mycelium as in the case of *Myrmecodia*.

C. longituba Chodat and Vischer. Chodat found in the swellings of this species in Paraguay nests of *Pseudomyrma chodati* Forel (Forel, 1920a).

C. miranda de Candolle and *C. hispidissima* de Candolle possess, according to Beccari (1884), similar myrmecodomatia; they form, together with *C. nodosa*, a special section of the genus (*Physoclada* A. de Candolle).

Verbenaceæ

Cosmopolitan, but mostly in tropical and subtropical climes. Represented by 900 species, belonging to 80 genera.

Clerodendron Linnæus. Tropical regions of the Old World. About 200 species.

C. myrmecophilum Ridley. Malay Peninsula, Sumatra, Borneo.

C. breviflos Ridley. Malay Peninsula.

C. fistulosum Beccari. Borneo.

These three species have normally hollow branches, which are often inhabited by ants (Beccari, 1884; Ridley, 1910; Shelford, 1916). According to Beccari and Shelford, the ant of *C. fistulosum* is *Camponotus (Colobopsis) clerodendri* Emery; it gnaws entrances to the hollow stem always directly below the insertion of the leaves, either on one or on both sides of each node; on plants free from ants, these spots are marked by a little circular patch of a texture and structure different from that of the surrounding parts. Beccari also describes and figures the internodes as markedly swollen, and more so towards their upper extremity.

An unidentified species of *Clerodendron* in the Belgian Congo also shelters ants inside its hollow branches (see above, p. 443).

Vitex Linnæus. Tropical regions of both hemispheres. With 120 species. Two myrmecophytic species have been mentioned as occurring in Africa, and probably some others also shelter ants inside their stem.

V. Staudtii Guerke. Togo, Cameroon, Spanish Guinea, Belgian Congo. Creeper with hollow stems and branches, which are inhabited by *Viticicola tessmanni* (Stitz) (see above, p. 447).

V. yaundensis Guerke. Cameroon.

Rubiaceæ

One of the largest families of plants: over 5000 species, classed under some 400 genera, have been described. They are cosmopolitan, though the majority are found between the tropics. About sixty-five species belonging to eleven genera present myrmecodomatia, this family thus containing by far the largest number of myrmecophytes.

Myrmecodia Jack.¹ Oriental Region, from CochinChina and the Malay Peninsula to New Guinea, northern Queensland, the Solomon and Fiji Islands. There are eighteen species. All are epiphytic, low shrubs, with rhizomes swollen into basal pseudobulbs or tubers, occupied by anastomosing cavities which communicate with the exterior by means of numerous pores and are often inhabited by ants; the apertures seem to be formed naturally, without the intervention of the ants, at least in certain cases.

Beccari originally (1884) held that the galleries of the swollen rhizomes were the work of ants; that it was impossible for plants to reach maturity without the intervention of these insects; that the tunnelling by them caused the tuber to grow enormously, while its weight was not proportionally increased, the galleries thus enlarging the absorbent surface of the rhizomes.² Later he altered his views somewhat, as can be seen in the following quotation from his 'Wanderings in the Great Forests of Borneo' (1904, p. 405):

At first I thought that the ants by the irritation they produced on young budding plants of *Myrmecodia*, favored the swelling of the base of the stem, and were the direct cause of such an hypertrophy. Further investigations and researches and the observations of Dr. Treub have, however, convinced me that from the very beginning these swellings appear independently of any action of the ants, and that when the latter are absent the tubers develop much in the same manner. I do not, however, think it equally certain that ants have no part in the formation of the internal galleries. My observations tend to prove that in some cases, in non-Bornean species of *Myrmecodia* (*M. alata* and *bullosa*), ants take an active part in the formation of the galleries and especially in that of the apertures which lead to them. But be this as it may, the hospitating Rubiaceae live on a footing of reciprocal utility or mutualism with their inhabitants, which act as a formidable army of defence, for no animal dares to meddle with a plant guarded by a host of biting ants, ready to assault the imprudent invader in myriads.

H. O. Forbes (1880 and 1885, pp. 79-82) and Treub (1883, 1888) raised young *Myrmecodia* from seed and found that the tuber is a normal production of the plant and that the galleried inner structure arises in the absence of ants. Treub's investigations are of such importance that they should be considered more in detail. He saw that soon after germination and before the first leaves are formed, the axis below the

¹Rumphius (1750, VI, p. 119, Pl. LV) first discovered the remarkable East Indian Rubiaceae with ant-tubers. He distinguished two kinds: "*Nidus formicarum niger*" (*Hydnophytum amboinense* Beccari) and "*Nidus formicarum ruber*" (*Myrmecodia Rumphii* Beccari). He believed that not only the swellings but also the entire plant were produced by the ants. Beccari (1884) has given a complete account of the earlier history of these plants; it contains very little of interest to the ecologist and entomologist.

²H. N. Moseley (1879, p. 389) had before expressed the opinion that in *Myrmecodia* and *Hydnophytum* "as soon as the young plants develop a stem, the ants gnaw at the base of this and the irritation produced causes the stem to swell; the ants continuing to irritate and excavate the swelling, it assumes a globular form, and may become larger than a man's head." He also believed that these plants cannot thrive without the ants.

cotyledons begins to enlarge and it is from this part of the plant that the whole tuber is produced. When the swelling is quite young the entire mass of cells, including the central bundle, is continuous; but when older, some of the central cells have dried up and thus form the first cavity whose inner walls are covered with a layer of suberose cells; later other galleries are formed, which at an early stage communicate with one another. Treub also apparently admits that the entrances to the cavities are produced by the *Myrmecodia* itself without any outside help. In his opinion, the tuber and inner labyrinth are normal ecological peculiarities of the plant, the latter being used for aerating purposes. The walls of the galleries are in some parts smooth and uniform, in others studded with little prominences, which Treub thinks are not, as originally supposed, glands secreting some fluid attractive to ants or absorbing organs for nutritive substances, but lenticels or rudimentary breathing organs. The ants he regards as mere opportunists who have taken advantage of the secure shelter afforded by the excavated tubers, but are of no visible utility to the plant.

G. Karsten (1895) also disclaims the supposed symbiotic relations between the *Myrmecodix* and ants. He believes, however, that the cavities have not only a respiratory function, but that their inner walls can also absorb transpiration water condensed inside the tubers during the cooler nights and at the same time assimilate certain dissolved nutritive elements introduced by the ants or found in the excrement of these insects.

Rettig (1904) agrees with Karsten and Treub in explaining the peculiarities of the *Myrmecodix* and allied genera on the ground of the physiological needs of the plant. He notes that these epiphytes are light-loving, thriving in nature on branches which are much exposed to intense sunshine or even on rocks; the galleries of the tubers are filled with air and act as aerating tubes, which isolate the inner tissues and prevent the plant from drying out. This author does not discard Treub's idea that the pimples on the inner walls may be for respiration; he even observes that there is undoubtedly a current of air through the apertures, since fresh air enters during the cooler nights and partly escapes during the day. He believes, however, that in many cases rain-water enters the cavities through the openings and is then absorbed by the tuber; he has shown experimentally that such absorption can actually take place.

Our knowledge of the *Myrmecodix* has been materially increased by Mische's (1911b) researches. According to his findings, the inner walls of the cavities of *Myrmecodia tuberosa* are, as a rule, clean; those in

certain portions are smooth, of a brownish-yellow color, never covered with fungi, and the pupæ of the ants are always kept in such galleries only; others are blackish, strewn with paler papillæ, the dark color being due to a covering of fungus. This growth occurs only in tubers occupied by ants and, when opened, such cavities exhale a fresh mushroom odor. It is evident that the tips of the hyphæ are cut off by the ants and in some places whole sods of these filaments are trimmed evenly, yet Miche believes that the insects do not feed on the fungus, but merely cut the hyphæ down because their growth would interfere with the ants' movements in the galleries. He thinks, however, that the mycelium grows on the excrement voided by the ants on the papillose portions of the walls only. The papillæ are evidently not rudimentary roots or root-buds, but Miche calls them haustoria or suckers, since he learned from experiment that parts covered with them readily absorb water, while the smooth portions do not. In wild and in cultivated specimens he often found rain-water accumulated in some of the cavities. He notes that the *Iridomyrmex* of *Myrmecodia* is seldom seen outside the galleries, unless the plant be disturbed, on which occasions the ants rush out at once. Their food was not ascertained, nor whether they come out at night. They seemed to him provided with very feeble weapons.

Concerning *Iridomyrmex myrmecodiæ* in the Solomon Islands, Wm. M. Mann (1909, p. 362) gives the following account:

This is one of the most abundant ants in the Solomons. It nests sometimes beneath bark or in crevices on standing trees, but usually in bulbs of an epiphyte, *Myrmecodia* species (?*M. Guppyanum*), which grows on the branches of several species of trees and is especially common on a lowland-inhabiting species of *Barringtonia*. It has been shown that *Myrmecodia* can thrive without the presence of ants, but I am sure that few of this species do, for among the many that I cut open, none were without them. Even very young bulbs, less than an inch in diameter, contained incipient colonies.

In a more recent paper W. M. Mann (1921, p. 406) mentions the common occurrence of various species of *Myrmecodia* and *Hydnophytum* in the Fiji Islands. Their bulbs are often inhabited by colonies of ants, *Iridomyrmex sororis* Mann, *I. nagsau* Mann, and its subspecies *allicola* Mann being the more common forms. *Pacilomyrma senireuxæ* Mann subspecies *myrmecodiæ* Mann and certain *Camponotus* and *Pheidole* also occasionally use such bulbs as nesting sites, though Mann remarks that many bulbs "contained no ants at all, but myriopods, spiders, scorpions, or geckos and their eggs."

Wheeler (1919, p. 111) records *Camponotus quadrisectus* (Smith) "from the distorted pseudobulb of a *Myrmecodia*" in Borneo and

Crematogaster difformis F. Smith subspecies *sewardi* (Forcl) was also described from a Bornean *Myrmecodia*.

M. armata de Candolle. Java. As Rettig remarks (1904, p. 12, footnote), this is evidently the plant so carefully investigated in Java by Treub, and originally called by him (1883) "*Myrmecodia echinata* Gaudichaud." Later (1888), Treub agreed with Beccari that his former identification was incorrect but claimed, apparently with reason, that his plant was not *M. tuberosa* Jack. It is the species used by Rettig (1904) for some of his experiments and the one studied by H. Mische (1911) under the name "*M. tuberosa* Beccari." Mische found most of his specimens inhabited by *Iridomyrmex myrmecodix* (Emery); in one locality, however, exclusively by *Camponotus maculatus* subspecies *pallidus* (Smith). Beccari (1884) also mentions the occurrence of *Iridomyrmex myrmecodix* in the tubers of Javanese "*M. tuberosa*" (= *M. echinata* de Candolle).

M. tuberosa Jack. Sumatra, Borneo, and probably elsewhere in the Malay Archipelago. Beccari (1884) found in Bornean specimens *Crematogaster difformis* Smith and Shelford (1916), also in Borneo, *C. difformis* and *Iridomyrmex myrmecodix* (Emery). Shelford mentions that both ants are by no means restricted to the tubers of epiphytic Rubiaceae, for they frequently nest in hollowed-out branches of various dead or living shrubs or trees.

M. bullosa Beccari. New Guinea, Amboina (G. Karsten, 1895). Inhabited by *Iridomyrmex cordata* (Smith) in New Guinea (Beccari, 1884).

M. Menadensis Beccari. Celebes. S. H. Koorders¹ gives the following interesting remark concerning this plant: "Especially common in the Minahasa in the lower plain to 1000 m. above sea-level in young forests, preferably in abandoned coffee-orchards. One sees there on most of the half-dead dadap trees (*Erythrina*) a number of these strange epiphytes. It is remarkable that as a rule I have found, on the same trees, one or more specimens of the following other curious myrmecophilous epiphytes with tuberous stem divided into chambers, viz., *Hydnophytum formicarum* Jack, *H. Selebicum* Beccari, *Polypodium sarcopus* DeVr. and Teysm. and *Polypodium carnosum* Christ, and of the most peculiar *Conchophyllum maximum* Karsten." Thus there seem to be regular "associations" of myrmecophytic epiphytes, in the sense plant ecologists use this term.

¹1898, 'Verslag eener botanische dienstreis door de Minahasa.' (Batavia), p. 497.

M. Rumphii Beccari. Amboina. Tubers inhabited by *Pheidole megacephala* (Fabricius) (Beccari, 1884). Merrill (1917, p. 489) positively identifies with this species Rumphius. "Nidus germinans formicarum ruber."

M. alata Beccari. New Guinea. One of the tubers contained *Iridomyrmex scrutator* Smith, *Pheidole megacephala* variety, and *Crematogaster* species (Beccari, 1884).

M. Antonii Beccari. Professor Wheeler has contributed the following note with regard to this Australian species: "While I was at Kuranda, in northern Queensland, during the winter of 1914-1915, Mr. F. P. Dodd collected for me in the vicinity of the village a number of specimens of *Myrmecodia Antonii*, all of which were inhabited by colonies of *Iridomyrmex myrmecodix* variety *stewarti* Forel, originally described from Torres Straits. The colonies were not populous and, as the ant is small and timid, I fail to see how it can protect the plant. This ant sometimes nests about the roots and leaves of other epiphytes. At Cairns, near Kuranda, I found a colony nesting under the leaves of a *Dischidia* that were applied to the branch of a tree. In northern Queensland both *Myrmecodia* and *Hydnophytum* are called the 'ant-house' by the colonists."

M. Goramensis Beccari. Moluccas. Tubers settled by *Iridomyrmex cordata* Smith (Beccari, 1884).

M. erinacea Beccari. New Guinea. *Crematogaster* species was found in the tubers (Beccari, 1884).

M. Albertisii Beccari. New Guinea. Tubers inhabited by *Iridomyrmex cordata* Smith (Beccari, 1884).

M. Dahlii K. Schumann. Bismarek Archipelago. Dahl (1901) found the galleries of the tubers inhabited by *Iridomyrmex myrmecodix* subspecies *decipiens* Emery and a subspecies of *Camponotus maculatus* (Fabricius); both ants were also found nesting in other locations.

M. pentasperma K. Schumann (erroneously quoted as *M. pentagona* by Forel). Bismarek Archipelago. The tubers were inhabited by *Iridomyrmex cordata* Smith and *I. myrmecodix* (Emery) (Dahl, 1901).

Myrmedoma Beccari. New Guinea. Contains two species: *M. arfakiana* Beccari and *M. Naumanni* Warburg.

Myrmephytum Beccari. Malay Archipelago. With two species, *M. Selebicum* Beccari, Celebes, and *M. Beccarii* Elmer, Sibuyan (Philippines).

Hydnophytum Jack. Oriental Region. Includes thirty-five species, with swollen excavated rhizomes as in *Myrmecodia*.

H. montanum Blume (= *H. formicarum* Beccari). Malay Archipelago, northern Queensland. Mische (1911b) found the tubers inhabited by *Iridomyrmex myrmecodix* (Emery) in Java; the walls of the galleries are in places covered with a fungus-growth similar to that of the *Myrmecodix*. Beccari (1884) mentions having found in the tubers *Iridomyrmex myrmecodix* (in Java) and *Crematogaster difformis* (in Borneo). This species was also studied by Treub (1883) and others.

H. petiolatum Beccari. New Guinea. Tubers inhabited by *Iridomyrmex cordata* Smith (Beccari, 1884).

H. amboinense Beccari. Amboina. Merrill (1917, p. 488) positively identifies with this Rumphius' "*Nidus germinans formicarum niger*."

Squamellaria Beccari. Fiji Islands. With two species. This is related to the foregoing four genera and may possibly be myrmecophytic in a similar way; it is not known, however, whether it has tubers.

Nauclea Linnæus. Tropical Asia, Malay Archipelago, islands of the Pacific. Contains forty species.

N. lanceolata Blume. Java. The branches present swellings inhabited by ants (K. Schumann, 1891b, p. 57, fig. 22B).

N. formicaria Elmer. Mindanao, Philippines. "Nearly all the twigs of the tree were teretely swollen, 3 to 7 cm. long and 1 cm. thick. These cylindrical portions were punctured and inhabited by small black ants" (Elmer, 1911, p. 990). I have examined a specimen collected by Elmer (cotype) in the herbarium of the Arnold Arboretum of Harvard University: the cylindric swelling is situated above the middle of one of the internodes and begins and ends abruptly, being very regular and slightly flattened on the two sides corresponding to the lower leaf-pair. On the same branch the two internodes above the swelling are perfectly normal. Professor Wheeler recognized in the remains of ants found inside the domatia a species of *Crematogaster* of the subgenus *Dccacrema*.

N. strigosa Korthals. Borneo and Luzon, Philippines. G. D. Havi-land (1887, p. 53, Pl. II), who has examined a number of herbarium specimens, writes that in most of them "some of the branchlets have hollow swellings which have been inhabited by ants." He adds: "I suspect that this plant is the *Sarcophelus macrocephalus* of K. Schumann, of which I have not, however, been able to find any description." *S. macrocephalus* was briefly characterized by K. Schumann in 1890; its branches present swellings inhabited by ants; it was found on Samar Island near Luzon, Philippines.

Nauclea strigosa has been made the type of a distinct genus, *Myrmeconauclea*, by Merrill who says (1920, p. 376) that "a certain percentage

of the branchlets always present hollow swellings, perforated on one side, which are inhabited by colonies of small ants."

N. celebica G. D. Haviland. Celebes. "The branchlets present numerous hollow swellings which have been inhabited by ants" (Haviland, 1897, p. 54).

N. cyrtopoda Miquel. Borneo, Sumatra, Java. The branches often have hollow swellings occupied by ants (Haviland, 1897, p. 57).

Uncaria Schreber (= *Ourouparia* Aublet). Tropical regions, mostly in the Old World. Contains thirty-four species.

U. africana G. Don. Tropical Africa, Madagascar, Comoros. The myrmecodomatia have been described above (p. 458).

Sarcocephalus Afzelius. Tropical regions of the Old World. There are thirteen species.

An unidentified species of *Sarcocephalus* from the Belgian Congo is myrmecophilous (see above, p. 460).

Duroia Linnæus fil. (= *Schachtia* Karsten; *Amajoua* Pœppig and Endlicher). Tropical South America. Includes ten species.

D. hirsuta (Pœppig and Endlicher).

D. petiolaris J. D. Hooker.

These two species have branches with spindle-shaped, hollow swellings which are inhabited by ants, species of *Azteca*, *Myrmelachista schumanni* Emery, and *Allomerus septemarticulatus* Mayr (K. Schumann, 1888; Emery, 1891).

D. saccifera (Martius) (= *Amajoua saccifera* Martius). Brazil. Two contiguous pouches, at the base of the leaf-blade, are often settled by ants (K. Schumann, 1888 and 1891b, p. 12, fig. 5B; Spruce, 1908).

D. dioica (Karsten) (= *Schachtia dioica* Karsten). Colombia. The original description says: "ramulis . . . ad apicem internodii inferioris elongati innovationum tumidis."¹ According to Huth (1887), Karsten did not find ants in these swellings.

Remijia de Candolle. South America. With fourteen species, only one of which is myrmecophytic.

R. physophora Bentham has two pouches, inhabited by ants, at the base of the leaf-blade (K. Schumann, 1890; Spruce, 1908).

Randia Houston. Tropics of both hemispheres, especially in the Old World. Contains 150 species.

R. Lujæ É. De Wildeman.

R. myrmecophyla É. De Wildeman.

¹Karsten, 1850, *Linnaea*, XXX, p. 157.

Both from the Belgian Congo; internodes swollen into spindle-shaped myrmecodomatia (see above, p. 465).

R. physophylla K. Schumann. Cameroon, Belgian Congo. Rudimentary pouches with a nectary, attracting ants, at the base of the leaf-blade (see above, p. 467).

Plectronia Linnæus. Tropical and subtropical parts of the Old World. Includes 200 species.

P. glabriflora (Hiern) of Tropical West Africa, *P. Laurentii* E. De Wildeman of the Belgian Congo, and some other species of Tropical Africa have swellings of the stems in which ants often nest (see above, p. 471).

Cuviera de Candolle. Tropical Africa. There are fourteen species, a number of which have swellings of the internodes inhabited by ants of the genus *Crematogaster* (see above, p. 488). Such myrmecodomatia are known with certainty for the following species:

C. longiflora Hiern. Cameroon.

C. latior Wernham. Belgian Congo.

C. Ledermannii Krause. Cameroon.

C. angolensis Hiern. Angola, Belgian Congo.

C. physinodes K. Schumann. Gaboon.

Psychotria Linnæus. A very large genus with over 400 described species and distributed throughout the tropics of the Old and New World.

P. myrmecophila Lauterbach and Schumann. New Guinea. A bush with pouch-like stipules; the margins are reflexed and the stipule itself much inflated; the cavity thus formed is divided into two by a median projecting carina; apertures are pierced through the wall and also through the inner partition. Remains of ants, together with coccids, have been found in these stipular pouches (K. Schumann and K. Lauterbach, 1901, p. 579, Pl. xxii).

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