MYRMECOPHILY

by

A. G. Ross Lowdon, M.A.

Edinburgh University.

Entered for Anderson Henry Prize.

June 1933.

1. INTRODUCTORY. . . . . Page 1

Historical 4

Ants and Plants 7

Classification of Myrmecophytes . 12

11. MYRMECOPHYTES 17

Polypodium and Lecanopteris . . 22

Korthalsia 24

Ficus Inaequalis 25

Cecropia 26

Triplaris 43

Acacia 45

Tachigalia 52

Macaranga 54

Cola and Scaphopetalum . . . 59

Barteria 59

Melastomaceae and Tococa . . 62

Dischidia 67

Cordia 70

Clerodendron 77

Vitex 79

Myrmecodia and Hydnophytum . . 84

Duroia 91

Plectronia . . . . Page 92

Cuviera 94

Ant-Gardens 96

111. MYRMECOPHILY. 99

Leaf Structures 99

Hollow Rhizomes 103

Myrmecodomatia in Stems and Branches . 104

Feeding Habits of Plant-ants . . 106

Advantages to the Plants . . . 121

Theories of Myrmecophily . . . 126

Critics of Myrmecophily . . . 136

Conclusion 142

Bibliography 144

1. INTRODUCTORY.

It is now at least three centuries since the attention of botanists and myrmecologists was first directed to the interesting phenomenon of ant-inhabited plants. The study of the subject, however, is still in such an incomplete state that even the terminology has not been standardised. The term "myrmecophily" necessarily implies a hypothesis to the effect that the plants have a biological interest in being visited by the ants (μύρμηξ = ant, φιλεῖν = to love). It has lately, however, been used more loosely by authors who do not admit that the relation between plant and ant is one of symbiosis. Such a practice leads only to confusion, and the term will be used here only where reciprocal benefit is implied. Ant-inhabited plants will be designated "myrmecophytes" or "ant-plants".

No adequate or standard definition of the term "myrmecophyte" has yet been formulated. The earlier writers, most of whom supported the theory of myrmecophily, accepted Schimper's (1888) * definition of ant-plants as "plants with adaptations

* Here and elsewhere in this essay the date after an author's name serves as a reference to the bibliography.

adaptations for attracting ants". When some doubt was thrown on the hypothesis of symbiosis this definition became untenable. Warburg (1892) proposed that plants associated with ants should be classified, according to the nature of their relation, as follows :

A) MYRMECOTROPHIC plants provide only food to the ants.

B) MYRMECODOMIC plants furnish only shelter to the ants' nest.

C) MYRMECOXENIC plants act as true hosts, providing for their ant guests both shelter and food.

He appears to have coined the term "Myrmecophyte" to cover all three groups. It is generally agreed, however, that this application is too wide, and that the term should be applied only to the second two groups. Warburg's three divisions have never passed into common usage. Ule (1906) chose to designate as ant plants "alle die Pflanzen die dauernd von bestimmten Ameisen-anten bewohnt werden". He excluded cases where the ants occasionally, and by accident, settle in normal leaf-sheaths, slits in the bark, dead branches, etc.

In the present very incomplete state of our knowledge concerning the feeding habits of plant-ants, it would seem inadvisable to make Warburg's distinction between Myrmecodomic and Myrmecoxenic plants. We know so little, indeed, about the

the sources of the ants' food that it is safer, provisionally, to make no references to them in a definition of ant-plants. We shall therefore take the term "myrmecophyte" to include all plants which present domatia in which certain species of ants make a more or less permanent abode.

The necessity for the stipulation that "certain species of ants" must inhabit the plant is dependent on the fact that only a small number of ants have become adapted to nesting in the domatia of ant-plants. Among these a distinction should be drawn between obligatory and facultative ant guests. Obligatory plant ants live exclusively in myrmecophytes; e.g. Viticicola tessmanni is never found away from its host plant Vitex Standtii: two species of Pachysima (P. aethiops and P. latifrons) are only found in association with various species of Barteria and Epitaberna. Facultative plant ants, on the other hand, are only occasionally or accidently associated with the plants, and are often found nesting in other situations.

The principal myrmecophytes will be described later, but meanwhile the general fact may be noted that all ant plants are perennials and of a woody texture. This is essential to ensure the permanency which the ants demand of their domatia, and the solidity which is required to protect their formicaries.

in some cases where the domatia are located on the leaves (e.g. Tococa) the protection is necessarily less permanent in the case of a single domatium, but new shelter is always readily available on the same plant. The majority of myrmecophytes are also glabrous.

HISTORICAL.

One of the earliest references to myrmecophytism was made by Michael Gehlerus in 1619; he referred to the way in which ants have come "to know plants". In 1651 Francisco Hernandez described one of the American ant-acacias as Arbor cornigera or the Huitzmamaxalli ("forked-thorn") of the Aztecs. He expressed the common belief of the time in the opinion that the ants are actually generated by the domatia. Rumphius, who described the Myrmecodiae in 1750, reversed the proceeding; he believed that not only the swellings but also the entire plant was produced by the ants.

The discussion of the problem of myrmecophily was initiated by Belt (1874); in his book "The Naturalist in Nicaragus" he described some ant-plants of South America, and expressed the opinion that the relation between ant and plant was one of symbiosis. Delpino, working independently, came to the same conclusion almost simultaneously. In this interpretation of

of the observed phenomena these writers were supported by most of the botanists who followed them in the nineteenth century. Beccari made a historic contribution to the subject in the second volume of "Malesia" (1884); in 1888 Schimper published "Die Wechselbeziehungen zwishen Pflanzen und Ameisen im tropischen Amerika"which has remained ever since the outstanding contribution to the subject; at the same period valuable work was done by Muller and Schumann (1888 and 1891). The one notable exception to this support of the hypothesis of symbiosis is found in the work of Treub (1882 and 1888): he confined his attention to Myrmecodia and Hydnophytum and argued, with the support of systematic observation and experiment, that the ants were parasites. He was careful to confine his conclusion also to the same two genera.

With the twentieth century we meet a new phase in the history of the discussion. After the year 1900 little serious support was given to the theory of reciprocal advantage as first enunciated; Ridley (1910) and Shelford (1916) alone added their half-hearted agreement. Buscaloni and Huber (1900), it is true, upheld symbiosis as an interpretation of the facts, but on slightly different grounds from those presented by Schimper and others. Spruce's paper, published in 1908, really belongs to the year 1869 when it was read before the Linnaean Society.

Had the Council of the Society not refused to authorize its publication because of certain references to the inheritance of acquired characteristics, the honour of inaugurating the discussion of myrmecophily might have belonged to Spruce instead of Belt, and the history of that discussion might have been very different.

Rettig (1904), Ule (1905 and 1906), H. von I hering (1907), Madame Nieuwenhuis von Üxkull-Güldenbrandt (1907), Fiebrig (1909), Wheeler (1913) and others assailed the theory of myrmecophily, and succeeded in demolishing many of the principal arguments advanced in its support. In 1920 Chodat and Carisso brought forward "Une nouvelle theorie de la myrmecophilie" but received only opposition and that principally from De Wildeman (1921).

A very valuable contribution to the subject was made in 1922 by two American writers, Bequaert and Bailey. The former published "A Review of African Myrmecophytes " and a "Synopsis of Recorded Myrmecophytes"; the latter called his article "The Anatomy of Certain Plants from the Belgian Congo, with Special Reference to Myrmecophytism". They worked in co-operation and produced between them, a complete review of the whole subject of myrmecophytism, besides making some very important contributions to our knowledge of the morphology and

and ecology of the African ant-plants. At the same time they emphasised the necessity of careful observation of the anatomy of the plants and the feeding habits of the ants before farther conclusions were drawn. Since then, contributions to various aspects of the subject have been made by Mobius (1925), Blatter (1928), Doctors van Leeuwen (1929), Wheeler and Bequaert (1929), Melin (1930) and others. None of these authors have supported the original hypothesis of symbiosis in any form.

In spite of the great weight of argument published in the last thirty years against the theory of myrmecophily, it cannot be said that the matter is by any means settled. The original hypothesis seems to have taken a very strong hold of the minds of botanists before arguments began to be adduced against it. Whereas logically it should be incumbent upon the protagonists of myrmecophily to adduce proof of their hypothesis, the historical development of the problem has resulted in the present position in which it is assumed to be incumbent upon the critics of that theory to disprove the assumptions made by the earlier writers.

ANTS AND PLANTS.

Myrmecophytism is only one example of the varied and often intricate relations which exist in nature between ants and

and vegetation. Some of the other types of relation have a close bearing on the subject of ant-plants; these will be given special emphasis in the following account of the various relations between ants and plants.

Ants are often found tending aphids, coccids and other insects for the sake of the sugary fluid which they excrete. The Hemiptera suck the juices of the plants on which they live, and the ants "milk" these insects for their anal secretion. This method of feeding has the advantage for the ants, over direct feeding on plant juices, that the supply is within easier reach and more abundant at any one time; the plant saps, moreover, undergo chemical changes in the digestive tracts of the Hemiptera which render them more suitable for the ants. The aphids and coccids are modified for this relation, and are protected by the ants from their many enemies, so that the relation is taken to be symbiotic. Since many plant-ants tend coccids this relationship is often of importance as providing a source of food from the host plant to the guest ant. Farther reference will be made to the matter after particular myrmecophytes have been considered.

Most of the wood-boring ants accomodate themselves to pre-existent galleries made by other insects, or attack dead wood only. Certain carpenter ants of temperate regions extend their

their burrows from dead into healthy wood (e.g. species of Camponotus). Though this clearly points the way to myrmecophytism, it is in the tropical and subtropical Pseudomyrminae that we find all transitional stages between the common wood-boring habit and the more specialized behaviour of nesting inside living, normal organs of plants and myrmecodomatia (Bequaert 1922). Bailey (1922) has demonstrated that, in the step from gnawing dead to gnawing living vegetable tissues, the ant is influenced both by the anatomical structure and the chemical composition of the plant.

The activities of harvesting and domestic ants concern us less. The "foraging" or "driver" ants are protective of vegetation, and others are of economic importance in that they excavate, transport and hasten the decay of organic substances. It has frequently been stated, without very convincing proof, that ants act as agents in the pollination of flowers; there is less reason to doubt their importance as distributors of the seeds of the plants. Neither of these functions, however, have any direct bearing on the problem of myrmecophily.

Ants are frequently observed visiting the extrafloral nectaries of certain plants. The term "extrafloral nectaries" includes all glands secreting saccharine substances located

located on the vegetative organs of plants. There is still considerable discussion as to their true significance - whether they subserve a physiological function or are adaptations for the attraction of ants. It has been suggested, as already pointed out, that all plants with extrafloral nectaries should be regarded as myrmecophytes. Though this extreme view has been accepted by very few naturalists, the fact remains that these organs occur on many plants which rank as myrmecophytes under the definition adopted in this essay. They serve as a source of food to the ants, and are therefore an important factor in the discussion of myrmecophily; the question will be reverted to at a later stage.

Not uncommonly ants shelter their brood within old galls produced by various insects. Certain species of ants, infact, are so frequently found in galls that this location of their nests has become part of their normal behaviour (Bequaert 1922). The importance of this habit with reference to myrmecophytism lies in a variety of reasons. In the first place the gall-inhabiting behaviour of ants is so like their habit of colonising regular myrmecophytes that it seems possible that the former may throw some light on the origin of the latter. Secondly, confusion between galls and true myrmecodomatia is quite probable, especially since the galls often have such

such regular shape and structure. Historic instances of such confusion are found in the cases of Ficus inaequalis, Clerodendron formicarum, and the ant-acacias of Tropical Africa. Finally, Bailey (1922) has shown that the activity of the ants in the myrmecodomatia of certain ant-plants results in the production of hyperplasias or abnormal tissues by the plant. In this respect the myrmecodomatia have a feature in common with the insect-galls.

The Attini of South America, otherwise known as the "leaf-cutting" or "parasol" ants have a double bearing on the question of myrmecophytism. In the first place they are serious enemies of tropical vegetation; when they attack a tree they leave it stripped of almost all its leaves. The protagonists of the theory of myrmecophily have contended that the main benefit which the plants derive from their guest ants is protection against the attacks of these Attini. In the second place they are all intimately associated with fungi which they cultivate on a substratum formed from the pieces of leaves they have destroyed. Belt (1874) was the first to appreciate this fact as indicating the truce significance of the leaf-gathering habit. The leaves are kneaded into a spongy mass in the ants nest; this is soon traversed in all directions by mycelial

mycelial threads from which little white bodies grow. These bodies have been termed by Möller "kohlrabi-clumps", and are described by Schimper (1898) as follows: " They consist of an agglomeration of short branches with nodelike or globular swollen ends and very rich protoplasmic contents. The kohlrabi-clumps are the most important, if not the sole, food of the ants, and represent a new structure which has arisen as a result of artificial selection exercised by the ants." Möller states that the ants cultivate the clumps by preventing vegetation sprouting of the fungus. Ants living in myrmecophytes are known to crop fungus growths in the domatia in a somewhat similar way. Whether they deliberately cultivate the fungus as do the leaf-cutting ants is open to doubt. Farther consideration of this question will be postponed till the problem of the feeding habits of plant-ants is discussed.

CLASSIFICATION OF MYRMECOPHYTES.

Several systems of classification of ant-plants have been adopted by various writers. Reference has already been made to Warburg's three groups: Myrmecotrophic, Myrmecodomic and Myrmecoxenic. Schumann (1891) favoured a somewhat similar division. Apart from the objection that it includes too many plants under the term myrmecophyte, it has the further disadvantage that the number of categories is so small that as

as a classification it scarcely serves its function of simplification.

Ridley (1910) and others have suggested a heirarchy of myrmecophytes in which these plants are arranged according to the degree of symbiosis between the ants and the plants. Ficus irregularis, according to Ridley, exhibits the most elementary stage in the development of myrmecophily - a temporary and accidental association of ants and plant. This is followed by a case such as Pachycentria where the roots are dilated and hollow for water storage. The ants take advantage of the suitable nesting place without offering any service in return- a type of relationship which is fairly common. He places next such cases as Korthalsia, Dischidia and the nest epiphytes Thamnopteris and Platycerium where the plants show no special adaptation for the attraction of the ants, but seem to derive a slight though unessential benefit from them, as by the deposition of nutritive substances near the roots. He confesses that he cannot understand the service which the ants render to such plants as Clerodendron, Lecanopteris, Polypodium, Myrmecodia and Hydnophytum, but seems to regard these plants as links in the chain which leads to the true myrmecophiles, e.g. Macaranga triloba. In some species of Macaranga there are adaptations whose sole purpose is to attract the ants, while

while the ants in return render a very necessary protection to the plant against predaceous caterpillars and insects. Ridley supposes that Cecropia adenopus and Acacia cornigera are also cases of true symbiosis.

Apart from the obvious objection that such a classification is teleological, depending as it does on the very information which would be a complete answer to the problem of myrmecophily, there is also the disadvantage that no hard and fast line can be drawn between the members of one category and those of the next.

Probably the best of the suggested classifications is that adopted by Spruce (1908). It depends on the location and type of the myrmecodomatia. It has the advantage that its categories are distinct and are not defined by teleological hypotheses. Bequaert (1922) points out that "The structures offered as myrmecodomatia by the ant plants show 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 ento,ophilous flowers to pollinating insects". The following types of myrmecodomatia may be distinguished:

1. The stems of the plant are externally normal, but hollowed out practically their entire length: Vitex Staudtii, Cecropia,

Triplaris and Barteria Dewevrei.

2. The stems present fistulose swellings.
   (a) in the middle of the internodes : Randia.
   (b) in, above or below the nodes : Cordia, Plectronia and Cuviera.
   (c) at the base of certain branches : Barteria fistulosa.
3. Fistulose and hollow shizomes : Polypodium, Lecanopteris and Myrmecodia.
4. Hollowed pseudobulbo : Schomburgkia.
5. Stipular thorns : Acacia.
6. Stipules persistent and modified : Macaranga.
7. Pouches at base of leaf blade : Tococa, Cola and Scaphopetalum.
8. Pitcher shaped leaves : Dischidia.
9. Swollen petioles : Tachigalia.
10. Inflated leaf-sheaths : Korthalsia.

The above classification is adapted from Bequaert (1922). The myrmecophytes named are given only as examples and are by no means exhaustive, though all the best known genera are assigned to their categories. It is questionable whether the section Physocladae of the genus Cordia should not be assigned to a separate category in view of the peculiar mode of formation of its domatia (vide infra).

These methods of grouping emphasise the great differences in the structural peculiarities shown by the various myrmecophytes, and also the various types of relation between the ants and the plants. It is thus made clear that each plant must be considered separately, and that generalisation is difficult if at all possible. In the following section of this paper the known myrmecophytes will be tabulated and described, Since none of the methods of classification have any distinct advantage which cannot be derived from the synopses given above, arrangement according to systematic sequence has been preferred. This practice has the recommendation that it employs an already established classification, and serves to compare and contrast, by juxtaposition, the structural peculiarities shown by members of the same families and genera. In the third section of the paper some generalisations will be made about the relations between ants and true myrmecophytes, and the various theories of myrmecophily and myrmecophytism will be reviewed.

II. MYRMECOPHYTES.

The phenomenon of myrmecophytism is found in so many different kinds of plants that no general statement can be made with reference to its occurrence and distribution in the plant kingdom. If, however, it is admitted that the Ant-acacias of the dry East African plains and Clerodendron formicarum of the savannah country are not true myrmecophytes, it can be said that myrmecophytism is found only within the tropics. One probable reason for this fact is that beyond these limits the temperature is not uniform enough throughout the year to permit of ants making their permanent abode in such thin walled domatia as the myrmecophytic plants afford.*

Even within the tropics, however, the proportion of plants permanently inhabited by ants is, comparatively, very small. Figures are not available for the New World, but Bequaert (1922) has estimated that in Africa, where approximately 30,000 species of flowering plants have been identified, some 42 species have been established as probable myrmecophytes. He adds that there are more myrmecophytes in other tropical regions but believes that the proportion is little if any larger. In the same paper he publishes a "Synopsis of Recorded Myrmecophytes" of which an abstract is given below. This appears to be a fairly exhaustive list of all the probable ant-plants that have been described in the history of the subject, and is of interest as

* The true ant-acacias of America would constitute the only notable exception to the statement that all myrmecophytes occur in the tropical Rain Forests.

showing the distribution of the phenomenon in the plant kingdom, as well as for reference purposes. Only one genus has been added to the list as published by Bequaert, viz. the genus Patima; one species of this genus was discovered to be myrmecophytic in 1922 by Mr Herbert Lang in British Guiana, and described by Dr. I. M. Johnston. Reference is made to it by Wheeler and Bequaert (1929). Some minor changes have been made in the number of species in other genera in the light of recent work. Where any genus is consistently found to be inhabited by a particular kind of ant (as is often the case), reference is made to the fact by appending the generic name of the ant. Finally a mark of interrogation or an alternative number of species indicates that the myrmecophytism in one or more of these species is doubtful.

PTERIDOPHYTA.

Family	Genus	No. of Species	Ants.
POLYPODIACEAE	Polypodium Linnaeus	5	
	Lecanopteris Blume	4	

MONOCOTYLEDONEAE.

Family	Genus	No. of Species	Ants.
PALMAE	Korthalsia Blume	6	Camponotus
	Calamus Linnaeus	1 (?)	
	Daemonorops Blume	1 (?)	

Family	Genus	No. of Species	Ants
ORCHIDACEAE	Diacrium Lindley	1 (?)	
	Schomburgkia Lindley	1 (?)	
	Grammatophyllum Blume	1 (?)	

DICOTYLEDONEAE.

Family	Genus	No. of Species	Ants
MORACEAE	Cecropia Linnaeus	15 or more	Azteca
POLYGONACEAE	Triplaris C.A. Meyer	10	Pseudomyrma
	Ruprechtia C.A. Meyer	1	
	Symmeria Bentham	1	
	Coccoloba Jacquin	1	
MYRISTICACEAE	Myristica Linnaeus	3 (?)	
MONIMIACEAE	Kibara Endlicher	1	
	Anthobembix Perkins	1	Iridomyrmex
LAURACEAE	Pleurothyrium Nees	3	
	Ocotea Aublet	4 (?)	
NEPENTHACEAE	Nepenthes Linnaeus	1 (?)	
ROSACEAE	Hirtella Linnaeus	1	
LEGUMINOSAE	Acacia Willdenow	4	Pseudomyrma
	Sclerolobium Vogel	1 (?)	
	Humboldtia Vahl	1	
	Schotia Jacquin	1 (?)	
	Tachigalia Aublet	6	Pseudomyrma and Azteca
	Platymiscium Vogel	15 (?)	

Family	Genus	No. of Species	Ants
MELIACEAE	Chisocheton Blume	1	
	Aphanamixis Blume	1	
EUPHORBIACEAE	Endospernum Bentham	2	
	Macaranga Du Petit-Thouars	8	Dolichiderus and Crematogaster
	Mabea Aublet	?	
STERCULIACEAE	Cola Schott and Endlicher	3	Engramma
	Scaphopetalum Masters	2	Engramma
FLACOURTIACEAE	Barteria J.D. Hooker	4	Pachysima
	Gertrudia K. Schumann	1 (?)	
MELASTOMATACEAE	Tococa Martius	c.35	Azteca
	Microphyxa Naudin	2	
	Myrmidone Martius	2	
	Maieta Aublet	8	
	Pachycentria Blume	2 (?)	
	Medinilla Gaudichaud	2	
LOGANIACEAE	Faqraea Thunberg	3	
GENTIANACEAE	Tachia Aublet	4	
APOCYNACEAE	Epitaberna K. Schumann	1	
ASCLEPIADACEAE	Dischidia R. Brown	5 +3 (?)	Crematogaster
BORRAGINACEAE	Cordia Linnaeus	5 or more.	Azteca and Pseudomyrma
VERBENACEAE	Clerodendron Linnaeus	4	Camponotus
	Vitex Linnaeus	2	Viticicola
RUBIACEAE	Myrmecodia Jack	18	Iridomyrmex

Family	Genus	No. of Species	Ants
RUBIACEAE (Contd.)	Myrmedoma Beccari	2	
	Myrmephytum Beccari	2	
	Hydnophytum Jack	c.35	Iridomyrmex
	Squamellaria Beccari	2 (?)	
	Nauclea Linnaeus	6 or more	
	Uncaria Schreber	1	
	Sarcocephalus Afzelius	1	
	Duroia Linnaeus fil.	4	
	Remijia de Candolle	1	
	Patima	1	
	Randia Houston	2 or 3	
	Plectronia Linnaeus	3 or more	Crematogaster
	Cuviera de Candolle	5 or more	Crematogaster
	Psychotria Linnaeus	1	

Very little is known about the relations between ants and many of the aforementioned plants, some of them being named only incidentally and by a single author as being myrmecophytic. Consideration of these cases would be unprofitable where no new material and evidence is available. The attention of botanists and myrmecologists interested in the relationship between plants and ants, has generally been focussed on a few of the better known myrmecophytes such as Cordia, Cecropia, Tococa and Acacia, and a certain amount of new data has become available on these

genera since Bailey and Bequaert reviewed the whole subject of myrmecophytism in 1922. In the following description of myrmecophytes, therefore, reference will be made only to those plants about which a reasonable amount of information is available, and special notice will be taken of the latest researches in each case. Nor will the work of the last decade be given special prominence only because it is more recent: it can in all fairness be claimed that it is also more thorough and systematic than most of the earlier researches (with a few exceptions which will be mentioned later). With the twentieth century it slowly became clear that further speculation on the subject of myrmecophily was only going to obscure the issue still more. The earlier writers had been more concerned to draw conclusions than to collect evidence. In 1922 Bailey and Bequaert made a strong appeal for careful statistical investigations of the problem, and for detailed anatomical study of the host plants. They themselves set a good example, which has been followed by the few scientists who have published papers on the subject since, and of whom it may fairly be said that they have shown more interest in collecting evidence than in drawing conclusions.

POLYPODIUM and LECANOPTERIS.

There appears to be some doubt whether these two genera are distinct. So far as myrmecophytic peculiarities are concerned they are very similar and may be described together. The six species of Polypodium which are found associated with ants

constitute the sub-genus Aspidopodium Diels (= Myrmecophila Christ). They are epiphytic ferns with creeping rhizomes. These rhizomes are swollen on the side which is not pressed against the support; the swelling is at first filled with aquiferous tissue, but this soon dries up and leaves the thick rhizomes tunnelled throughout their whole length. Ants (usually Technomyrmex or Iridomyrmex) pierce entrances and inhabit these cavities.

The most famous of these myrmecophytic species is Polypodium sinuosum Wallich. Yapp (1902) described this plant and expressed the opinion that, while the aquiferous tissue of the rhizomes is probably developed originally as a water reservoir, its early disappearance may indicate a change of function. He suggested that the cavities formed may serve to aerate the stem, and also to a slight extent assist the absorption of water. Ridley (1910) pointed out that the plant is exceptionally susceptible to drought. "As a water reservoir, therefore," he wrote, "the rhizome (at least in its present state, with the ant galleries replacing the original large-celled tissue) must be considered a failure." He could observe no advantage accruing to the plant from the presence of the ants, and notes especially that protection is neither necessary nor given.

It is probable that the same conclusions are valid for the other species of Polypodium and Lecanopteris.

In this, and in the other descriptions which follow, any

evidence as to the advantage to the plant from the ant-plant relationship is of great importance, because this aspect of the problem is one of the main stumbling blocks of the Theory of Myrmecophily. Here as elsewhere, however, in this section, no conclusion will be drawn with reference to the theory of the relationship. The evidence will be summarised and the various theories discussed in the third section of the paper.

KORTHALSIA.

This genus is confined to the oriental region. All its 20 species are rattan-palms but only a few of these are myrmecophytic. In these the ligule of the leaf base, instead of forming a close tightly-fitting sheath, is transformed into a bulky sheath or ochrea which is usually somewhat round or oblong. This ochrea is frequently perforated and inhabited by ants which are usually of the genus Camponotus.

Beccari (1884) observed several species of this genus, and describes them with Myrmecodia and Hydnophytum and other plants as being truly myrmecophilous.

Ridley (1910) opposed this view, in the following words: "It appears to me very probable that no special kind of ant haunts these Korthalsias, but that any ant whose habits induce it to adopt this class of dwelling may do so. The primary use of ochreae is undoubtedly to throw off rain from the base of the young bud which it at first covers, and thus it is not in any way

a modification for the benefit of the ants. The only possible advantage that the ants could bring to the plant would be to defend it against the attacks of caterpillars and other insects." His observations show that "the ants are not always present yet the plant unprotected does not suffer from their absence." He summed up these considerations in the words "there is no special modification which can only be accounted for as of use to ants; there is no clear benefit to the plant from the presence of ants at all"; and concludes that the plant is not myrmecophilous. These arguments are of interest in view of the fact that Ridley strongly supported the theory of myrmecophily with reference to other genera, notably Macaranga.

FICUS INAEQUALIS.

This plant was described and figured by Schimper (1888) as a myrmecophyte. He had observed swellings on the branches which he supposed to be myrmecodomatia. Ridley (1910), however, kept the same tree under observation in the Botanic Gardens at Singapore, and was led to the conclusion that it was not a myrmecophyte. "I have since constantly examined this tree and others in the Gardens," he writes, "and find that these swellings and the ants have quite disappeared. The branches were, I believe, swollen by some disease or abnormality of growth, and in course of development split, and the holes produced were occupied by ants."

This case is mentioned here, not because there remains any doubt of the accuracy of Ridley's conclusion, but because the mistake is important evidence of the unreliability of the deductions of the earlier observers. It shows that even Schimper, who is still considered to be the authority on myrmecophily, did not hesitate to weave his inferences round a single tree.

CECROPIA.

The genus Cecropia Linnaeus includes the most historic of all the myrmecophytes and is also of especial interest because it appears to exhibit the highest developments of the relationship between ants and plants, whatever the significance of these developments may be.

The genus occurs throughout tropical America from Mexico to Brazil, but not all of the 30 or 40 species are myrmecophytic. The trees are slender and candelabra-shaped and are often referred to as the "imbaubas" as they are called in Brazil, or the "cétícos" as in Peru. They generally grow in dense groves but are also found on the roadside and elsewhere as secondary growth. Some myrmecophytic species prefer the alluvial woods which are inundated when the rivers are in flood, and a few thrive even in the true inundated forest where they stand for a great part of the year many feet deep in water (Wheeler and Bequaert 1929).

The myrmecophytic species have hollow stems, in which nests of Aztecas are almost invariably found; they also produce food-

bodies known as "Müllerian bodies" which are eagerly collected and devoured by the ants. Wheeler described Cecropia adenopus as follows (quoted from Bequaert 1922):

> "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 prolifer-

ates 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."

Before considering the details of the morphology and ecology of these myrmecophytes we shall review the historical advance of our knowledge of the subject, and also name the different species of Cecropia, referring to any distinguishing features of special interest.

Historical.

The first mention of the inhabitation of Cecropiae by ants appears to have been made by Marcgravius in 1648. In 1874 Belt initiated the discussion of myrmecophily; among other mrymecophytes described in his book "The Naturalist in Nicaragua" are the Cecropiae. He described how the ants gained access to the internodal cavity by making a hole from the outside, how they burrowed through the partitions, and also how they tended coccids "which suck the juices from the tree, and secrete a honey-like fluid that exudes from a pore on the back and is lapped up by the ants." He made no record of the food bodies. These were discovered by Fritz Müller, after whom they were named by Schimper. Müller discovered also the oval depression or prostoma in which the ants invariably make their entrance apertures, and described the origin of the colonies of Azteca in Cecropia adenopus.

The historical significance of Cecropia is largely due to

Schimper's careful investigation, the results of which were published in 1888. He described in detail the "Müllerian bodies" growing on the trichilium, and expressed the opinion that they are originally mucus- or resin-glands which have become highly modified as an adaptation to the ants. He made a careful examination of the groove to be found above the insertion of every leaf, and showed that it ended in a diaphragm at the top where the hard and tough elements of the wood were completely absent. He concluded that this was also an adaptation for the benefit of the ants who in return protected the host plant against phytophagous insects and particularly the leaf-cutting ants; these latter, Müller and Schimper were agreed, are the chief enemies of the Cecropiae against which the protection by Azteca is devised.

Later observers have offered many objections to the interpretation of the facts favoured by Belt, Müller and Schimper. Eminent among these have been Ule (1905, 1906), Rettig (1904), H. v. Ihering (1907), K. Fiebrig (1909), Wheeler (1929), Bequaert (1922, 1929), and Bailey (1922 a, 1922 b). Their various contributions to the subject will be mentioned later. Rettig called attention to the presence on the leaves of Cecropia adenopus of bead-like glands containing proteids and fatty oils. These are also collected and used as food by the ants.

The ant found in association with Cecropia is invariably a species of Azteca, and very often Azteca muelleri Emery, which

Müller and Schimper wrongly named "Azteca instabilis".

Species of Cecropia.

Cecropia adenopus Miquel (= C. peltata Vellozo, nec Linnaeus) This plant is common on the east coast of Brazil. Wheeler's description of the species has already been quoted. Most of the early observations were made on C. adenopus, which has long been considered as one of the most classical illustrations of myrmecophily. That it is not, however, completely typical of the Cecropiae is shown by the following quotation from Wheeler and Bequaert (1929): C. adenopus "is peculiar in that its normal ant inhabitant, Azteca muelleri Emery, establishes in the bole of the older plants a spindle shaped carton nest of such dimensions that it is marked on the outside by a distinct swelling of the stem. No such swelling was ever seen by the junior author in any of the Amazonian species although many thousands of specimens of half a dozen species were carefully examined".

Von Ihering regarded this so called "metropolitan nest" as a gall. Wheeler showed that this could not be so since there was n hypertrophy of the tissues, the wall of the trunk where it encloses the nest showing no structural modification except a bending outward of the woody fibres. This, he concludes, is the natural result of the weight of the superposed trunk and crown of foliage on the circular area weakened by the gnawing of the ants.

C. angulata Bailey. British Guiana.

This species is very similar to C. adenopus except in respect of the "metropolitan nest". Bailey (1922 b.) made a detailed study of it, adding thereby a valuable contribution to the subject of the Cecropiae and their relation to ants. His observations, which will be mentioned later, led him to the conclusion that the ants were parasites on the host plant.

He describes the tree as being 10 to 25 metres high with large lobed leaves which change considerably in appearance as they grow, and with large male and female inflorescences. Its fistulose stems were inhabited by four distinct species of Azteca, and coccids were found in the domatia.

C. leucocoma Miquel (= C. arenaria Warburg)	Brazil
C. obtusa Trécul	Brazil

Both the above species, which are very similar to C. angulat were found to be inhabited by Azteca ants (Wheeler and Bequaert 1929).

C. robusta J. Huber	Lower Amazon
C. bifurcata J. Huber	Brazil
C. lastivirens J. Huber	Brazil
C. paraensis J. Huber	Lower Amazon
C. distachya J. Huber	Vicinity of Para.

These five species were recorded as "myrmecophilous" by J. Huber in 1910.

C. lyratiloba Miquel South Brazil

- was studied by H. von Ihering. It possesses trichilia and was inhabited by a species of Azteca.

C. riparia "Warburg" Brazil

C. ficifolia "Warburg" Rio Acre, Brazil

C. montana "Warburg" Peru.

The above three species were found by Ule to be inhabited by Aztecas and to possess trichilia.

C. sciadophylla Martius Brazil

Ule recorded C. sciadophylla Mart. var. decurrens as myrmecophytic. He found it to be inhabited by Azteca ants. Bailey (1922 b.), however, regards it as non-myrmecophytic because it lacks trichilia and food-bodies (although it possesses a prostoma), and because he never found Aztecae in the hollow internodes.

C. mexicana Hemsley Brazil

This species possesses no trichilia but was observed by Ross in 1909 to be inhabited by ants.

Many other species of Cecropia possess trichilia but this alone is not sufficient evidence to warrant the conclusion that they are myrmecophytes.

Fiebrig's (1909) observations were made in Paraguay on a plant which he calls "Cecropia peltata Linnaeus", but which Bequaert (1922) concludes was identical with C. adenopus of Brazil.

Domatia and Prostomata.

The domatia in the hollow stem are quite simple. The cavity

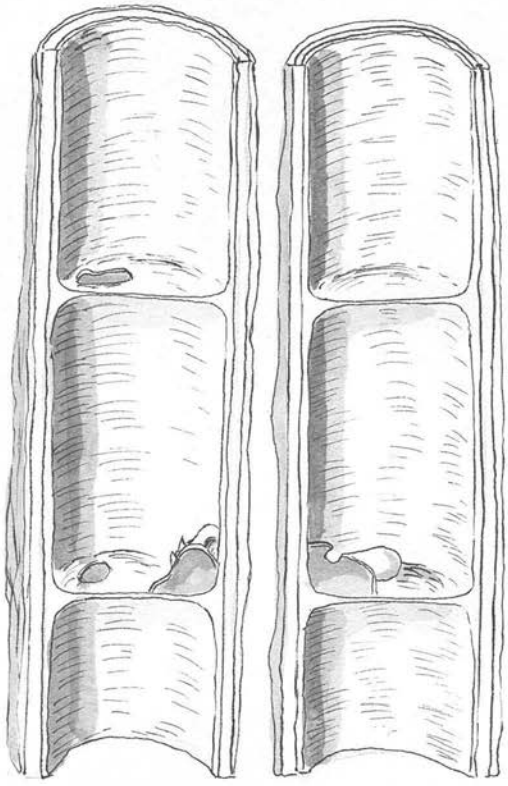

Fig. 1. Cecropia adenopus Miquel.

Portion of a young stem split longitudinally. Central hollow with septa perforated by the ants, and structures made by them. Natural size.

(After Schimper, 1888).

traverses the centre of the stem and is slightly wider above, corresponding to the increasing thickness of the growing apex. It is divided by nodal partitions. (See Fig. 1) There is no question of this cavity being an adaptation for the ants; this Schimper (1898) himself admits: "It represents rather a feature that is common to many other plants, and may be explained on the mechanical principle of construction as being the method of producing the greatest resistance to bending with the least expenditure of material."

The prostomata, however, are not so easily explained. Above the insertion of every leaf there is a shallow verticle groove. This groove ends just below the next node by expanding into a roundish depression. The external depression corresponds to an internal one so that the wall is very thin at this point, and especially so at the top of the groove where it is a mere diaphragm. Schimper (1888) showed that the hard and tough elements of the wood were absent from the tissue of this diaphragm - i.e. there are no fibrovascular bundles, collenchyma, lignified parenchyma etc. (See Fig. 2) It is always at this spot that the ants bore through into the internal cavity.

Schimper recognised the fact that the groove is originally caused by the pressure of the axillary bud, but maintained that the terminal diaphragm is a highly specialised adaptation to the ants, being the result of natural selection.

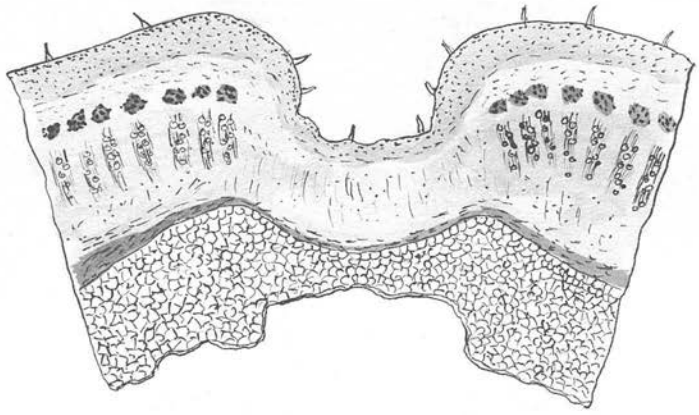

Fig. 2. Cecropia adenopus Miquel.

Part of transverse section of wall of internode showing "prostomata". Slightly enlarged. (After Schimper 1888).

Rettig (1904) and Fiebrig (1909) maintained that the prostoma is merely the youngest or less highly differentiated portion of the groove. Rettig adds that the ants perforate the highest part of the groove not so much for mechanical reasons as because they are deterred from excavating at a lower level by the occurrence of "laticiferous vessels" which are absent in the prostoma. Fiebrig maintains that the pits cannot be regarded as adaptations to the ants, because openings are often made to the exterior from the inside by ants which have entered a new internode through the nodal partition; and because these openings are often made irrespective of the situations of the pits.

Bailey (1922 b.) made a careful histological study of the mature and developing grooves. He concluded that the whole groove is a potential prostoma, that tougher and denser tissues extend in it from below upwards after the initiation of secondary growth, and that the ants excavate the apertures before this reinforcement has progressed very far. It is important to note that Schimper, assuming Bailey's observations to be correct, was arguing from false premises. He failed, apparently, to examine the developing groove, and was led therefore to the false conclusion that - "The tissues internal to the groove resemble those of the parts that are not exposed to pressure except the original pit, which increases in circumference after the pressure has ceased and at the same time is further modified." (Schimper 1898)

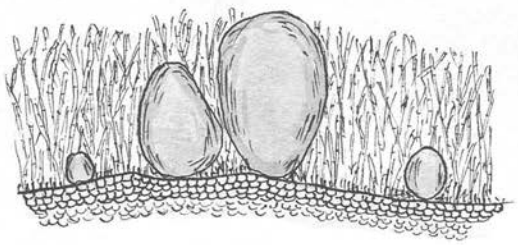

Fig. 3. Cecropia angulata Bailey.

Portion of trichilium showing food bodies and enveloping mat of hair. x 43.

(After Bailey, 1922 b).

Bailey's evidence is supported by the fact that he observed as many as five exits at different levels in one groove on a young plant; each aperture had been excavated by a different queen ant. These observations were made on C. angulata. To forestall the possible criticism that in this species the whole groove has become adapted to the ants Bailey points out that in the non-myrmecophytic C. sciadophylla the diaphragms are even more tenuous, being composed only of extremely thin layers of delicate parenchyma. He is led to the conclusion that the diaphragm is merely a "structural peculiarity produced by the presence of the axillary bud, which is utilised by the ants in their parasitism upon the plants".

Bequaert (1922) notes that the cells of the peripheral layer of medullary tissue in the myrmecodomatia of certain Cecropiae are filled with a translucent amorphous material which he calls the "amber-coloured substance", and discusses as a possible source of nutrition for the ants, coccids and fungi.

Food Bodies.

The food-bodies, as has been stated, were first discovered by Fritz Müller after whom they were named "Müllerian bodies". They grow on the trichilium or cushion-like mat of hairs which is situated at the base of each petiole, and are small bead-like structures, white in colour and, when ripe, lying loose among the hairs. (See Fig. 3) They are removed and eaten by the ants as soon as, or even before, they are mature, with the result that they are

never visible on an inhabited plant. They are richly packed with fat and protein, and are continuously being produced in large numbers.

Schimper (1888) declared that these bodies are metamorphosed glands which have become highly specialised as adaptations for the allurement of ants. While this view was accepted by all who believed that the relationship between the ants and the plants was symbiotic, it was later strongly opposed by Rettig (1904) and others who, although admitting that the bodies are metamorphosed glands, contended that they cannot be considered as adaptations to the ants, mainly on the ground that similar bodies are found on other non-myrmecophytic plants. Ule expressed the opinion that the expenditure of carbohydrates and nitrogenous substances contained in these corpuscles is not compensated for by the protection which the ants afford to the plants. Whatever their real function, they clearly serve as an important source of food to the ants, especially on those plants which grow in the inundated forest.

The Ants.

The ants which inhabit Cecropiae are almost invariably species of Azteca of which Azteca muelleri Emery at least may be considered as obligatory.

When the queen ant enters the cavity of a young plant she invariably does so by making a "stoma" in one of the prostomata.

She then seals the opening with a layer of triturated pith, and it subsequently becomes occluded by callus (Bailey 1922 b.). Müller, Von Ihering and Fiebrig infer that the queen feeds on medullary tissue, while Von Ihering adds the opinion that the luxuriant growth of callus is due to the stimulus of some substance excreted by the queens.

Bailey points out that these conclusions are drawn from the fallacious premises: (1) that the queen must feed during the two or three months of isolation. There is evidence, he says, that the female ants can do without food for the greater part of a year while they are founding their colonies.

(2) that tissues which are gnawed or excavated by ants are eaten by them. Bailey's own investigations lead him to very different conclusions. "The so-called stomatomes, upon which Müller and Von Ihering place so much emphasis, are not uncovered and cut back by the queens until just before the first workers are ready to emerge from the nest, nor do they excavate the medullary tissue to any considerable extent except when in search of material with which to block up the newly formed entrance aperture." With reference to the luxuriant growth of callus, supposed by Von Ihering to be produced by chemical stimulation, he finds that homologous structures can be produced by purely mechanical injuries.

Several queen ants may each start a colony in one of the

internodes of the same tree. Von Ihering supposed that the primary colonies so formed fuse to form one large community, after all except one of the queens has been killed. Wheeler doubts the possibility of such a fusion. The fact remains, however, that one large community is always eventually formed.

The feeding habits of the ants constitute an important aspect of the problem of myrmecophytism. On Cecropiae there can be no doubt that they eat the Müllerian bodies, and that they obtain a sugary exudate from the coccids which they tend (see below). Von Ihering and Fiebrig maintain that the imagines feed also upon the succulent medullary tissue in immature internodes. Bailey denies this, expressing the opinion that the excavation of the medullary tissue is only "house cleaning".

Coccids.

Belt, Müller, Üle, and others observed that the ants tended coccids in the domatia of the Cecropiae. Fiebrig (1909) asserted that these insects "in keinen direkten Verhältnis zu diesen Ameisen stehen". Bailey (1922 b.) found that the ants are extremely solicitous for the safety of the coccids, and has observed the ants in artificial nests to "spend hours in tending and stroking the coccids and in feeding upon their sugary exudates". He concludes that "it cannot be doubted that the miniature milch cows are an important source of liquid carbohydrates for the ants".

It is interesting to note that in the African ant-plants,

such as Barteria, Plectronia and Cuviera, the pits in which the coccids lie are located on the side walls of the domatia. In Cecropia angulata, on the other hand, they are found on the nodal partitions. These nodal partitions consist of five distinct layers which Bailey (1922 b.) describes as follows:

> "The soft, internal layer, which is provided with strands of conducting tissue and which is fed upon by the coccids, is separated from the external layers of porous medullary tissue by two layers of dense thick walled tissue. The ants remove the two external layers and cut circular pits in the underlying sheets of horny sclerenchyma. The coccids sit in these pits and thrust their setae into the succulent tissue which is thus exposed."

Von Ihering (1907) suggested that the pits are made by the coccids, but that this is not the case is evident from the fact that the sucking mouth parts of these insects could scarcely excavate the dense sclerenchyma of the partitions, and also from the fact that Bailey has observed the ants making the pits.

Protection by Ants.

Protection of the host plant by the inhabiting ants is the only considerable service that has been supposed to accrue from the ants to the plants. Since the relation cannot be supposed to be symbiotic unless the plant derives some benefit, it is very important that evidence should be considered as to whether this

service is really rendered or, if rendered, of any real importance. The evidence with reference to Cecropiae will be summarised here, though no general conclusions will be drawn at present.

Belt (1874) first suggested that the guest ants of Cecropiae protected the host plants against the leaf-cutting Attines. Müller (1880) and Schimper (1888) enlarged on this hypothesis, contending that the inhabiting ants protect the leaves against all phytophagous insects, but especially against the leaf-cutting ants, which they supposed to show a preference for the leaves of the Cecropiae. They found that the plants which were colonized by Aztecas were unmolested by Attine ants, whereas uninhabited individuals were more or less completely defoliated by them. They admit that in the coldest weather the tree may be exposed to attack, because the Attine ants are much less sensitive to the cold than the Aztecas.

Rettig(1904),Ule(1906),von Ihering(1907), Fiebrig (1909), Wheeler, and many others have opposed this view, contending that the early writers exaggerated both the destructiveness of the Attine ants and the protection afforded by the Aztecas.

Bailey (1922 b.) summarises their evidence as follows:

(1) Möller notes and the above writers (including Bailey) confirm that the leaf-cutting ants feed upon a great variety of plants, and show no particular preference for the foliage of Cecropia.

(2) Von Ihering estimates that 183 nests of Attine ants consume

no more foliage in a year than does a single cow in the same time.

(3) In many cases the inhabited myrmecophytes grow in inundated regions and swamps where there is no danger from the leaf-cutting ants.

(4) The young developing Cecropia is not inhabited or protected by its putative guardians.

(5) It has been shown that plants which are not inhabited by Aztecas may remain unmolested by Attas for long periods, and that trees which are inhabited may be seriously injured by phytophagous insects and sloths.

There is no evidence in support of the argument that juvenile species may be immunised by special protective devices. Belt and Schimper admit having seen young myrmecophytes defoliated, and Bailey showed by experiment that the Attine ants showed no preference for the older plants (1922 b.)

Melin (1930) adds further evidence against the tenets of the earlier writers with the remark: "My observations concerning certain myrmecophytic Cecropia species entirely corroborate the statements of v. Ihering and Fiebrig. Notwithstanding the occurrence of numerous obligatory ants (Azteca) several Cecropias of Roque in the Eastern Andes of Peru showed numerous traces of gnawing on the leaves."

In his argument that the Azteca-Cecropia relationship was on of symbiosis, Schimper placed great emphasis upon the discovery,

in the Corcovado, near Rio de Janeiro, of a "species of Cecropia devoid not only of the ants but also of the entrance-door (i.e. prostomata) and of Mueller's corpuscles". He inferred that these "adaptations for the attraction of a defending army of ants" are in this case unnecessary, because the plant is protected by a waxy coating which prevents the leaf-cutting ants from climbing its stem. The plant at least was uninhabited and uninjured. Schimper's explanation, though possible, is by no means the only possible one. The case may be contrasted with the following record by Bailey (1922 b.).

> "Cecropia sciadophylla Mart. var. decurrens Snethlage is not colonized by Aztecas, but ... is provided with conspicuous and highly differentiated prostomata. The external surfaces of the plant are scabrous and afford a firm foothold for ants, as evidenced by the fact that several species of these insects were seen climbing its stems and branches. This species of Cecropia is no more subject to defoliation by Attas than is Cecropia angulata. That the leaves may be utilized in the construction of fungus gardens is shown by the fact that, when cuttings from plants of various ages are placed near nests of Atta cephalotes, the ants frequently transport a portion of the foliage into their subterranean dwellings."

Bailey's non-myrmecophytic example provides at least as

convincing evidence against myrmecophily, as does Schimper's in favour of a symbiotic relationship between plant and ant.

TRIPLARIS.

This genus of the Polygonaceae is found in Tropical South and Central America. It is represented by ten species all of which have hollow internodes inhabited by ants. The branches, however, are not inflated.

One of the earliest accounts of myrmecophytism in the genus Triplaris was published by Robert Schomburgk in 1838 for the species T. Americana Linnaeus. He describes the tree, which he found common on the sandy banks of the inland rivers in Guiana, and often overtowering the other vegetation; and continues:

> "The uncautious 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."

Bequaert (1922), from whom the above quotation is taken, also repeats the observations made by Weddel in 1849 in which he records finding species of Triplaris inhabited by an aggressive Pseudomyrmine ant.

Schimper (1898) expresses the opinion that the dwelling in Triplaris is no more an adaptation to ants than that of Cecropia, but that the entrance aperture may safely be described as such. He points out that the plants bear no food bodies but that extra-floral nectaries are to be found on the leaves. Üle (1906) mentions the exits, and emphasises the destructiveness of the ants: "die Ameisen erhalten auch dauernd das innerste Mark des ganzen Stammes als Gang, von dem einzelne Seitengänge nach aussen führen, frei. Selbst auf dem Boden verkehren diese immer kampfbereiten Tierchen, und zerstören dort im Umkreis von einige Metern alle aufwachsende Vegetation."

Spruce (1908) makes the interesting observation that some of these trees "seem to try to grow away from the ants - growing to great length by bending over or hoisting themselves up into the adjacent trees by crooking their branches". The following notes are also of interest.

> "Triplaris surinamensis Camb. and T. Schomburgkii Benth., as well as the other arborescent Polygoneae, have slender elongated tubular branches, often geniculate at the leaf nodes, and nearly always with perforations, like pinholes, just within the stipules of each leaf, which are the sally-ports of the garrison, whose sentinels are besides always pacing up and down the main trunk..... I suspect that the remote progenitors of these ants have at first sheltered in

the ocrea (sheathing stipule) which is so characteristic a feature of the Polygoneae; but having found the wood soft and thin and the pith easy to scoop out, have made their more secure abode within the stem and branches."

Wheeler has pointed out that some isolated Triplaris trees stand with their bases in water throughout the rainy season, and that it is therefore difficult to understand how the ants manage to exist. He suggests that the ants may remain rather dormant or find some hitherto unknown food supply on the foliage. The real answer is more probably supplied by Bailey's observation (see Bequaert 1922) that the cavities of Triplaris contain great numbers of coccids from which the Pseudomyrmae obtain at least much of their food.

ACACIA.

In considering myrmecophytism in the genus Acacia it seems advisable to consider separately the Acacias of the Old and New Worlds. All the evidence points to the fact that while the bull-horn acacias of Central and South America are true myrmecophytes, the species of the genus which occur in association with ants in Tropical Africa cannot be included in the same category.

The acacias of Africa often have abnormally swollen thorns which may or may not be inhabited by ants. These swellings may be produced by, or for, the ants, or they may be true insect galls. The evidence in favour of the former hypothesis is so

meagre, and that in favour of the latter so considerable (Bequaert, 1922, synopsises this evidence), that these Acacias may fairly safely be dismissed as non-mrymecophytic.

There is even less doubt that the Acacias of Central and South America are true myrmecophytes.* The name "bull-horn acacias" is frequently applied to these species, because of the similarity of a pair of their stipular thorns to the horns of a bull. These thorns are swollen and sometimes flattened: they are usually hollowed out by ants which pierce an entrance below the tip of the thorn, more rarely near its base, and build their nests inside. The young leaves bear at the tips of their pinnae, minute bright yellow food-bodies (Beltian bodies) which are eagerly collected by the ants and carried away to be eaten. The plants differ from other myrmecophytes, according to Bequaert (1922), in that they all grow in dry or semi-desert regions. Fiebrig (1909,) however, who studied A. cavenia Hooker and Arnott in Paraguay, points out that this tree, in common with other species of Acacia, is protected against the ground-haunting Atta by the fact that it grows only in situations which are constantly liable to inundation. It is not clear how these two observations are to be reconciled. Comparatively little serious attention has been paid to these myrmecophytic Acacias, for all their fame as ant-plants, and

* Note: The best known species of these Acacias have been called A. cornigera, A. sphaerocephala and A. cavenia. There appears, however, to have been some confusion in the classification of the genus.

there appears to be much need for further investigation.

Domatia.

It is of interest to note that in 1651 Hernandez believed, in accordance with the ideas of his time, that the thorns themselves generated the ants. In 1874 Belt recorded finding Pseudomyrmine ants on an Acacia tree: "The branches and trunk are covered with strong curved spines, set in pairs... These thorns are hollow, and are tenanted by ants that make a small hole for their entrance and exit near one end of the thorn, and also burrow through the partition that separates the two horns; so that the one entrance serves for both." In another case he found a tree to be inhabited by a species of Crematogaster. These ants make their entrances near the centre of one thorn of each pair, and not near the end like the Pseudomyrma.

Schumann (1902) appears to believe that the cavity is actually made by the ants who eat the soft pith away. He describes the formation of the domatia as follows:

> "Sie (die Ameisen) beissen an der Spitze eines der beiden Dornen, aber auf der Unterseite, so dass keinen Regen einzudringen vermag, an einer verdünnten Stelle ein elliptisches Loch, fressen den weichen Inhalt des noch grünen Dornes aus und befördern ihn nach aussen."

There is some disagreement as to whether the domatia are not originally, as in the case of the African Acacias, insect galls. The latest and weightiest evidence, however, suggests that this

is not so.

Fiebrig (1909) states that the thorns in which the ants take up their abode have frequently been already hollowed out and furnished with apertures of access by lepidopterous larvae. The spaces, moreover, are not confined to the thorns but extend also into the stem, and are in both situations excavated, whether by ants or caterpillars, at the expense of the living tissues of the tree.

Chodat and Carisso (1920) developed the same idea into a theory of myrmecophily. They studied the same species as Fiebrig (A. cavenia), but went even further in their conclusions:

> "Ici encore l'excitation au développement exagéré de la stipule est fournie par une piqûre d'insecte; on peut suivre pas à pas l'infection, oeuf, larve et la progression vers la stipule qui s'acroît corrélativement, finalement la sortie de l'insecte par un trou d'épine. L'hypertrophie de ces stipules n'est donc pas due, comme le pensait Fiebrig, à une influence atmosphérique, mais elle constitue une galle, comme le sont les formicaires des Cordia, et qui est secondairement habitée par les fourmis."

This view was strongly opposed by De Wildeman (1921) who, while admitting that larvae etc. are often found in the hollow domatia, contended that the enlargement of the spines is not always due to the presence of a guest of any kind. He grew, in the

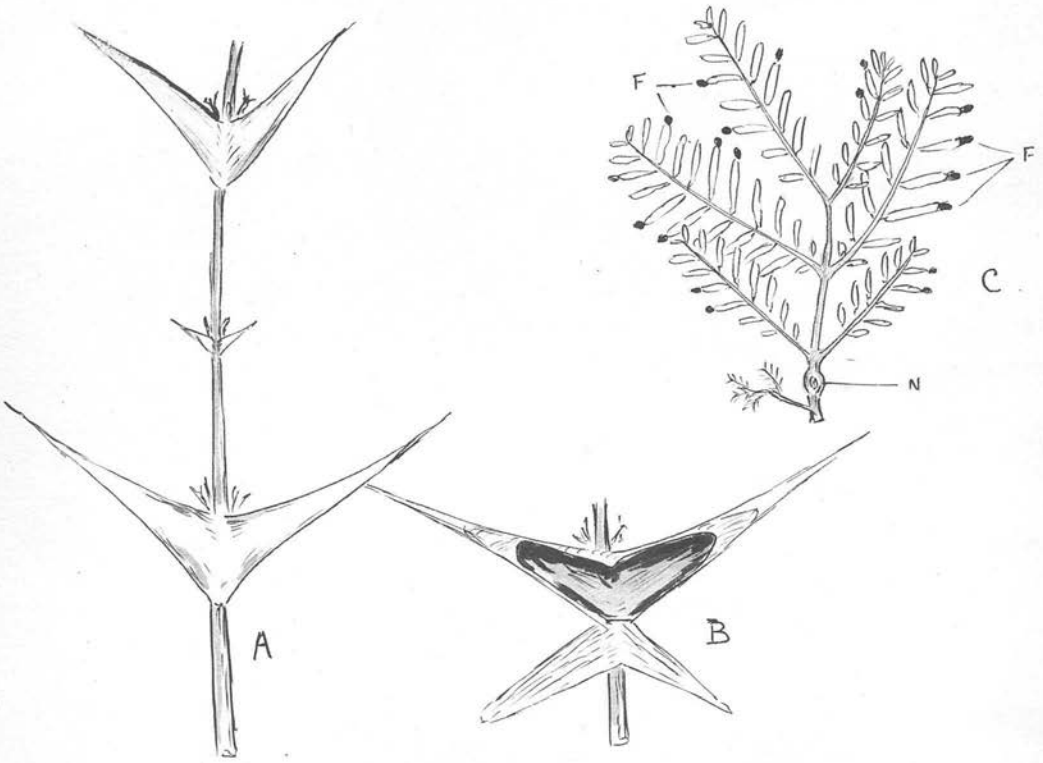

Fig. 4. Acacia cornigera.

from the Royal Botanic Garden, Edinburgh.

A. Part of stem with thorns.

B. Same as A with thorns opened to show hollow domatium. The section cut away has not been removed but allowed to hang down. The cavity is seen to be common to the two thorns.

C. Leaf with nectary (N) on petiole and Belt's corpuscles (F) on leaflets.

Botanic Gardens of Brussels, an Acacia which he calls A. cubensis. The thorns, he says, showed a tendency to swell soon after their first appearance.

"Quand elles sont encore vertes, elles renferment au centre une sorte de moelle lâche qui, petit à petit, disparait en suite de l'augmentation - de volume, et laisse une cavité dans laquelle il n'y a pas trace d'insecte. Quand les épines sont adultes, que la feuille est tombé, il n'y a pas d'overture à ces stipules; elles ne deviennent pas, dans ces conditions de culture, des domaties. Ici donc le renflement et le creux sont formés sans la présence de l'insecte perceur, ni de la fourmi habitante."

Bequaert (1922) and Bailey (1922 b.) express the conviction that the bull-horn acacias are true myrmecophytes, and that the domatia are not usually ant galls. Bailey at least bases his opinion on actual observation. Figure 4 shows drawings from a plant of Acacia Cornigera in the Royal Botanic Garden of Edinburgh. It will be seen that the thorns are large and hollow though it may safely be assumed that no insect has had access to them.

The Ants and their food.

The ants found on the American Acacias are usually Pseudomyrma, though Crematogasters are sometimes found to inhabit all the thorns on a single tree. The tree provides two sources of food for the ants. Belt (1874) describes these as follows:

"At the base of each pair of leaflets, on the mid-rib, is a crater-formed gland, which, when the leaves are young, secretes a honey like liquid..... At the end of each of the small divisions of the compound leaflet there is, when the leaf first unfolds, a little yellow fruit-like body united by a point at its base to the end of the pinnule. Examined through a microscope, this little appendage looks like a golden pear."

In the leaf figured from Acacia cornigera it will be seen that the nectary is situated on the petiole. The food bodies are very similar to those found on the Cecropiae (Müllerian bodies), but are called, after their discoverer, "Belt's corpuscles" or "Beltian bodies". They are rich in oil and protein and are eagerly collected, when ripe, by the ants.

Schimper (1888) and others 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 in size and, when not removed by the ants, finally drop off. (Bequaert 1922). According to Belt they do not all ripen at once but successively, so that the ants have a continuous supply of food for some time after the new leaves are formed. Schimper regarded these bodies as proof of the symbiosis between ant and plant. "They are distinguished," he

writes, "from all known glands by definite characters - larger size, longer duration, richness in proteids, easy severance when touched - all of which features may, with as much certainty as is possible in such cases, be regarded as adaptations to ants." (Schimper 1898).

Belt believed that the ants paid for their food and lodging by defending the tree, especially against the leaf-cutting ants. He grew plants from seed in his garden and found that, being unprotected by Pseudomyrma, they were soon completely defoliated by Attine ants; he adds also the statement (1874): "I have never seen any of the trees out on the savannahs that are guarded by the Pseudomyrma touched by them (i.e. the leaf-cutting ants), and have no doubt the acacia is protected from them by its little warriors."

Other writers in the nineteenth century supported him in this view and although some doubt has been thrown on it more recently, there appears to be no statistical evidence to disprove it. Careful investigation, however, might very probably show that the protection afforded has been very much over-emphasised; this assumption is warranted by the fact that such has been found to be the case in respect of Cecropiae, Cordiae, Tococa and many other well known myrmecophytes.

EX BIBL. UNIV. EDINBURGEN

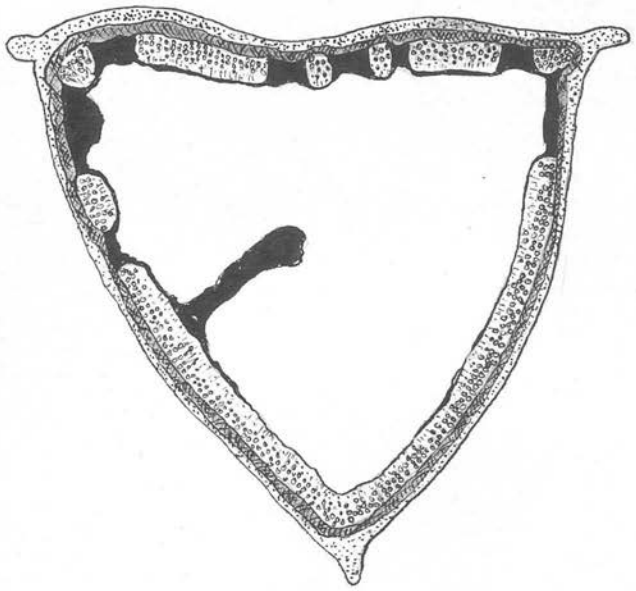

Fig. 5. Tachigalia Paniculata Aubl.

Transverse section of petiole of vigorous sun plant, showing medullary cavity, primary rays (black), and portion of carton partition; from plant colonized by Pseudomyrma maligna: x 6.

(After Bailey, 1923).

TACHIGALIA.

Little attention was paid to this myrmecophyte until Bailey published a detailed account of its morphology and ecology in 1923.

The genus was described by Aublet in 1775; its name is derived from "tachi", the word used by Indians of the Guianas to designate stinging ants. Two species are mentioned by Spruce (1908) as having inflated petioles inhabited by ants, viz. T. caripes Spruce, and T. ptychophyxa Spruce. Both occur in Brazil, and have trigonous petioles most of which are dilated at the base into a fusiform sac. Ule (1906) also mentions one species as being myrmecophytic, and cites T. spicata Aublet as "ein ameisenfreie Art", whose continued existence he takes to disprove the contention that myrmecophytes require any protection.

The following is a synopsis of the salient points in Bailey's paper (1923), which refers to the species T. paniculata Aublet.

He is of the opinion that the hollow triangular foliar axis of Tachigalia can be explained in the same way as Schimper explained the domatia of Cecropia and Triplaris - on the mechanical principle of construction as being the method of producing the greatest resistance to bending with the least expenditure of material. The internal cavity is merely a concomitant of the excessive enlargement of the pith. (Fig. 5)

In the competition in tropical regions between insects for nesting places, fierce conflicts are waged for possession of the

hollow foliar axes of Tachigalia. The obligatory ants found in the domatia are usually Pseudomyrma. The first inhabitants, however, are in most cases not the ants but beetles. Eventually, however, a queen ant succeeds in raising a brood in a petiole not visited by beetles. The worker ants swarm over the plant, kill or drive out all the beetles and take possession of all the domatia. "The beetles eat the parenchyma of the wide primary medullary rays, utilize it in the construction of their puparia, and solicit and obtain liquid carbohydrates from herds of coccids which graze upon it. The ants also feed upon this tissue vicariously through the intervention of coccids, and utilize it in the construction of carton partitions." The coccids, that is to say, once tended by the beetles, become the spoil of the victors.

The gnawing of the ants in the petiolar cavity stimulates the formation of amber coloured parenchyma. When Aztecas are in possession of the domatia they excavate pits in the walls of the petiole and rachis and often perforate the walls altogether. From examination of the trophothylaxes of the Pseudomyrmine larvae (vide infra), Bailey concludes that the ants do not feed directly upon the ray tissue but only vicariously through the intervention of coccids. He shows, in the same way, that these ants also eat the coccids or at least feed them to their larvae, adding: "It is significant in this connection that, although the coccids are thereby considerably reduced in number they never,

so far as we have been able to determine, are entirely exterminated. A sufficient number of adults survives for replenishing the herd."

He could find no evidence to indicate that Tachigalia needs the protection of Aztecas or Pseudomyrmas, or that such protection would be afforded if needed. Further, he admits no logical argument for assuming that the hollow foliar axes and the strands of amber coloured parenchyma are allurements for attracting ants. "Their presence may satisfactorily be accounted for as due to necessary anatomical, physiological, and mechanical adjustments." Lastly there is no reason to suppose that the structural peculiarities are initiated by ants or by gall forming insects. Bailey concludes, therefore, that the relation is one of parasitism in which the insects avail themselves of the structural peculiarities of the plant in a singularly efficient manner.

MACARANGA.

The genus Macaranga De Petit-Thouars is found over the tropical and subtropical regions of the old world. It includes about 170 species of which a number are myrmecophytic.

Among the myrmecophytic species there are two main types. In both types the stem of the young plant is hollowed by the disappearance of the pith, leaving a cavity in which the ants live. The ants enter and leave these domatia by holes perforated in the side of the stem at irregular intervals, one or more in each

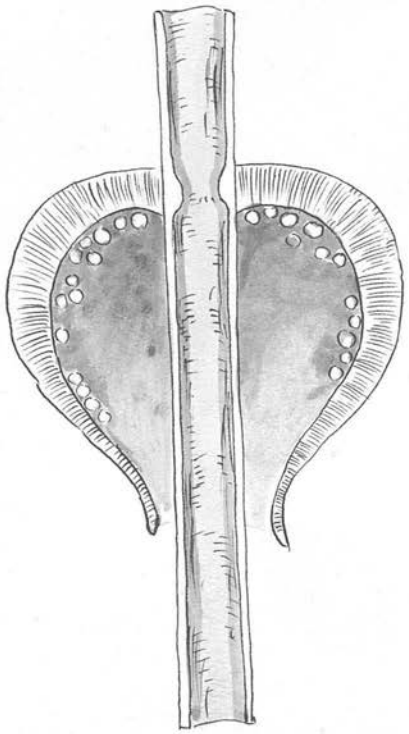

Fig. 6. Macaranga triloba (Reinwardt).

Section of bud-bract and stem showing food-bodies. (After Ridley, 1910).

internode. The ants perforate the nodal septa so that the internodal cavities are all in communication. In adult trees they have usually abandoned the hollow in the main trunk, and are to be found only in the ends of the branches. The inhabiting ant is generally a species of Crematogaster.

In the myrmecophilous species the buds are protected by an opposite pair of triangular or lanceolate sessile leaves or bud-bracts. In most of the species the young stem and leaves have a waxy coating, and on the margins of the young leaves red cyclindrical nectaries are borne. These drop off as the leaf attains its full development, leaving no trace (Ridley 1910).

In other respects the two types will be described separately.

M. triloba (Reinwardt). Malay Peninsula and Archipelago.

M. Griffithiana Mueller. Malay Peninsula.

M. Hulletii King. Malay Peninsula.

M. Hosei King Malay Peninsula.

In these four species the bud-bracts, after the expansion of the bud, do not fall off but are reflexed and continue to grow. As they bend back their tips come into contact with the stem and are tightly appressed to it so that a ringlike pouch is formed which almost completely surrounds the stem. (Fig. 6) In the hollow thus formed the ants may shelter themselves and their larvae. On the underside of the bracts are borne many white globular or pear-shaped bodies. These food-bodies are much sought for by the ants, and are carried away by them to the nest in the hollow stem

where they are fed to the larvae. The food-bodies are not found on the underside of the leaf of the four species of Macaranga at present under discussion: nor are they to be found on non-myrmecophytic species (Ridley 1910).

The following description of the development of M. triloba is of interest, since the development of the relation between plant and ant even in a single case is significant in discussion of the theory of myrmecophily. It is taken largely from Ridley (1910).

The stem of the seedling is at first solid, slender and woody and containing a small pith. As the plant grows the internodes become succulent and swollen with the maximum dilatation midway between the nodes. The pith disappears in these swellings leaving hollow parts separated at first by transverse bars, but later forming a continuous cavity.

The ants enter the lower internodes shortly after the hollows form, and, as the plant grows, the ants perforate the nodal septa and inhabit the upper internodes: only the terminal internode is uninhabited. The apertures are usually made in a shallow groove on the side of the internode further from the leaf; there may be none, or one, or more, on a single internode. The first perforations are of course made from the outside, but some of the higher apertures may later be made from the inside of the stem. There is no nest, properly speaking, and no material brought from

the outside except the food bodies, which are laid beside the heads of the larvae, and a few coccids, which are introduced while young and still small enough to pass through the apertures.

As the tree develops, the lower internodes become thicker and more woody, the apertures are closed, and the ants forsake their cavities for the newer hollows in the branches. The queen is usually found in the lowest inhabited internode..

The development of the bud bracts has already been described. The food bodies resemble those on Cecropia and Acacia and probably have a similar origin. Nectaries are borne where the veins end on the margins of the young leaves. Ridley states, however, that the ants pay no attention to these organs which fall off when the leaf is mature.

M. hypoleuca (Reichenbach fil. and Zollinger). Malay Peninsula, Sumatra, Borneo.

M. caladifolia Beccari. Borneo.

M. formicarum Pax and O. Hoffmann. Borneo.

These three species also have hollow stems settled by ants. The internodes are slightly more swollen especially in the young plant. The main difference between this and the previous type, however, is to be found in the bud-bracts. In the three species under discussion the bracts are lanceolate and erect: they are persistent also but bear no food-bodies. White and globular food bodies are found, however, on the backs of the young leaves be-

tween the raised veins. They are most plentiful on plants not settled by ants and have been seen carried about between the mandibles of these insects (Beccari, 1904; Ridley, 1910; Shelford, 1916; Bequaert, 1922).

Ridley regards all the six species described as exhibiting a symbiosis between plant and ant which is as complete as possible. He regards the domatia, the persistent bud bracts, and the food-bodies as adaptations for the attraction of ants. He supports his contention by pointing out that in the non-myrmecophytic species of Macaranga the stems are never hollowed out, the leaves possess no nectaries, the leaves and stem are never covered with a waxy secretion, there are no food bodies, and, in the majority of cases, the bud bracts are not persistent. The ants serve the plant by defending it against phytophagous insects and caterpillars. Unprotected plants, he avers, always look shabby and weak and have gnawed leaves: no plant is ever attacked, on the other hand, while it is protected by ants. He sees a significant connection, moreover, in the facts that it is the growing point and young leaves that require protection, and that it is the young branches which the ants inhabit. No serious attempt has been made to refute these conclusions.

Bequaert (1922) describes a third type of association between Macarangas and ants, but is not sure that it is a case of true myrmecophytism. He examined two species from tropical

Africa, M. saccifera Pax, and M. Schweinfurthii Pax. These he found to have persistent pouch-like stipules, which, in the case of M. saccifera, were found on several occasions to be inhabited by Crematogaster ants. Since no young or pupae were present, however, he concludes that the ants were using stipules merely as temporary shelters.

COLA and SCAPHOPETALUM.

In these two genera from the family Sterculiaceae, are included a few myrmecophytic species - two or more in each genus. The domatia take the form of a pair of small pouches at the base of each leaf blade. These pouches protrude on the upper surface, but are entered from the under side. They are only occasionally found to be occupied by ants, and these, when present, seem to offer no protection to the host plant, being of a small and timid species. Schumann (1891) regards the pouches as myrmecodomatia-adaptations to ants. De Wildeman (1921) admits that there is "malformation héréditaire", but sees no reason to talk of "adaptation".

BARTERIA.

Barteria is the only genus of the Family Flacourtiaceae which is definitely known to contain true myrmecophytes. Bequaert (1922) names six species as being myrmecophytic, and states that these are, together with those of Scaphopetalum, the commonest and most widely distributed of African ant-plants. Its guest ant,

Pachysima, is found only where Barteria occurs, viz. over an area stretching from the mouth of the River Niger over the Congo basin. Bequaert further asserts that this genus of Pseudomyrmine ants is almost restricted to the hollow stems and swellings of various Barteria, its only other known habitat being the caulinary swellings of Epitaberna myrmoecia in Cameroon.

The domatia in Barteria may take the form of hollow swellings on the stems, or of unswollen uniformly hollow stems and branches. These two types are found in Barteria fistulosa Masters, and B. Dewevrei De Wildeman and Durand respectively.

Barteria fistulosa.

This plant is a bush or small tree with horizontal branches having upturned leaves. Most of its branches are deciduous, the separation from the main stem taking place by a histological process similar to that which causes leaves to fall.

The lateral branches may be described as being of 2 kinds:

a) The great majority are sterile. These present a swelling which starts suddenly near the base and tapers away towards the end of the branch. Except in very young plants these swellings are nearly always hollow and inhabited by ants.

b) At certain seasons of the year there are found on the older trees a few flowering branches. These present no swelling but are often hollow and inhabited by ants.

In the sterile branches the cavity develops naturally as the pith in the swelling dries up. In the flowering branches the pith

is excavated by the ants. In both types the entrances are made in the soft walls by the ants, which are usually large and black belonging to the species Pachysima Aethiops (Emery). These ants are aggressive and have a painful sting: they attack any intruder and, according to Bequaert, constitute an effective defence against phytophagous insects and caterpillars. They often keep an area of ground for 9 or 10 feet round the tree barren of all growth, probably by nipping the young shoots. Bequaert suggests that this may constitute an advantage to the plant by removing competition.

Several queen ants may start colonies on the same tree but these colonies eventually fuse leaving only one queen alive. By the time that there is only one large community of ants the domatia have been enlarged to such an extent that each lateral branch forms one continuous gallery.

Whether the ants get all their food from the plant is very doubtful, but Kohl has seen the worker ants licking nectaries at the insertions of the leaves, and coccids are found in depressions in the walls of the domatia. It is possible that the ants attend these insects for the sake of their sugary excretions (Bequaert, 1922; Bailey, 1922 a.).

Barteria Dewevrei.

The lateral branches of this species are feebly branching and irregularly spreading, giving it a very different appearance

to B. fistulosa. No swellings are found on the branches, but they are completely hollow except the extremities of the young branches: these are filled with young green pith which soon dries up. The entrances are not numerous, and are usually located on the upper side of the branch, a short distance above the insertion of a leaf. The domatia shelter Pachysima or Crematogaster ants and a few coccids which are usually found in small scar-like depressions in the wall (Bequaert 1922).

One side of the myrmecodomatium is usually thinner than the others and is nearly devoid of vessels. Both the entrance apertures and the pits in which the coccids lie are located on this wall. The mouth pieces of the coccids are, according to Bailey (1922 a.), embedded in callus-heteroplasias which develop where the pits are made. He compares these callus formations to those that occur in Cuviera, and adds; "That the lateral pits are excavations made by the ants, and not depressions made by the collapse of delicate cells underlying the coccids, is indicated by the structure of the tissues upon the margins of the pits." If this is true it would appear, by analogy, that the ants solicitously tend the coccids for their own advantage in Barteria as in Cuviera.

MELASTOMACEAE and TOCOCA.

Tococa is a genus of the family Melastomaceae. There are several genera in this family containing myrmecophytic species,

and in most of these (with the notable exception of Pachycentria where the ants inhabit the hollow roots) the myrmecodomatia take the form of pouches on the leaves. The following description is from Melin (1930).

"Myrmecophytic Melastomae are generally bushy plants with numerous slender stems, growing on the outskirts of inundated areas as well as on firm ground on the edges of forests, and in sparsely treed woods. The oval leaves of the Melastomae, being easily recognised by their numerous parallel transverse veins, are furnished at the base of the laminae or on the petiole with a swelling resembling a sac and generally double, which opens on the underside of the leaf in the angles of the veins on both sides of the midrib. The sacs in question, that are often equipped with a thick bristly hairiness, are found fairly regularly but vary considerably in size in the same plant. Smaller leaves, especially such as grow closely beneath an inflorescence, often lack sacs. Extra-nuptial nectaries and so called 'food bodies' are wanting, or at least scarcely noticeable. Obligatory ants.... chiefly consist of species belonging to the genera of Allomerus, Pheidole, Crematogaster and Azteca."

Bequaert (1922) states that, with the exception of Pachycentria, all the myrmecophytic members of the family Melastomaceae are restricted to the neotropical region.

In 1775 Aublet pointed out that Tococa guianensis was sometimes called a "nid-de-fourmis", on account of the obligatory ants that inhabit the sacs of the leaves. He 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: it would appear from his description that the ants also inhabit the stem of the plant (Bequaert, 1922; Melin, 1930): Martius mentioned the genus as being associated with ants, but Schumann (1888) was the first scientist to make a systematic study of these myrmecophytes. He judged the pouches to be an adaptation acquired through natural selection, refuting Beccari's (1884) suggestion that they serve as a kind of nutritive organ.

Spruce (1908) describes the sacs on the leaves of various species of Tococa, and expresses the opinion that the sacs developed when the ants perforated the axils and sucked the juices, adding that the process tends to be transmitted by inheritance. He supported this view with the observation that the first leaves of young Tococa plants, and the lowest leaves of each ramulus of the adult plants have either no sac or only the slightest rudiment of one.

This explanation of the peculiar structures was refuted by Wheeler and Bequaert (1929). Their description of the myrmecodomatia in Tococa is worthy of quotation.

"The myrmecodomatia in this genus (Tococa) are protruding

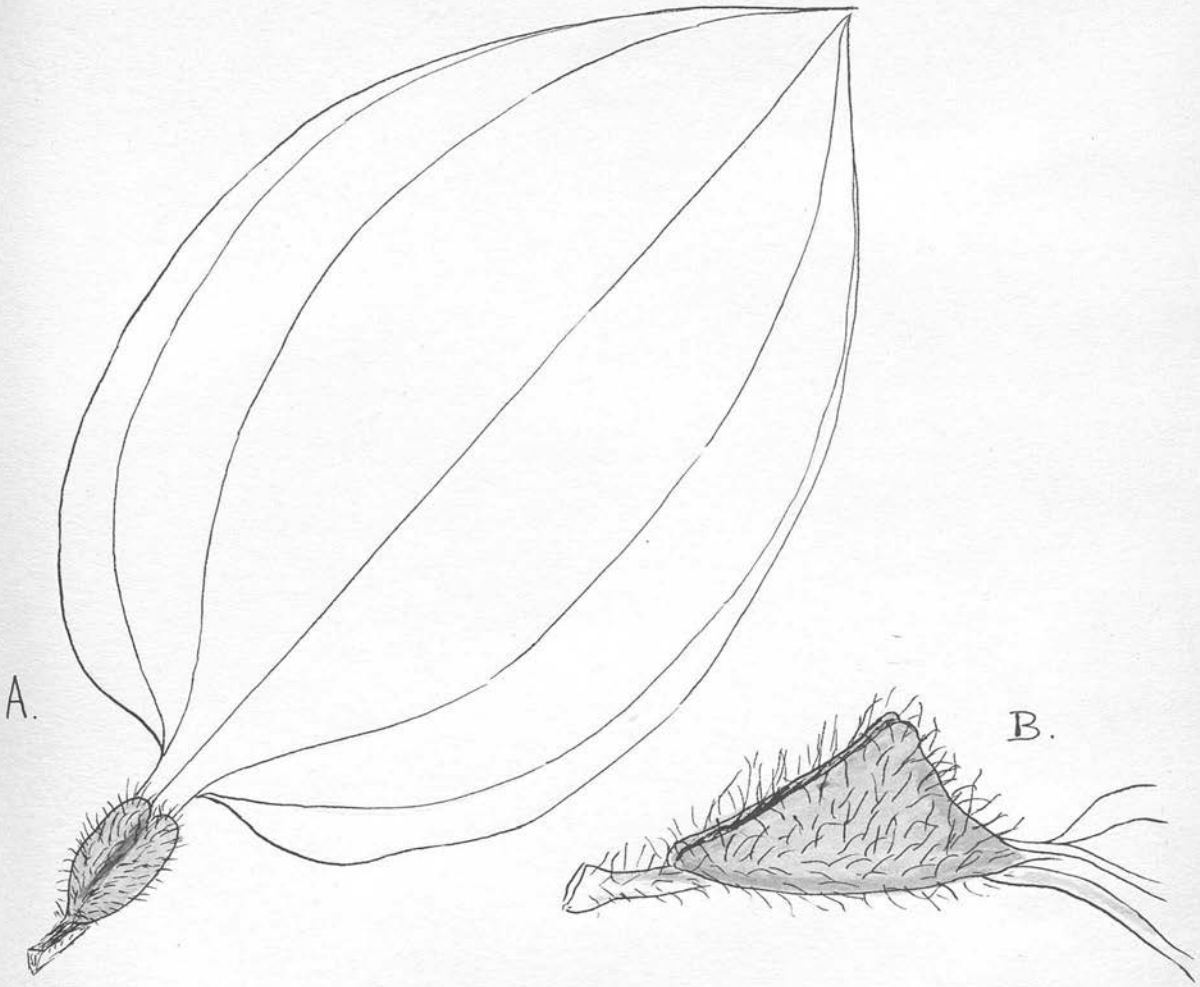

Fig. 7. Tococa formicaria Martius.

A. Leaf from the upper side x 2/3

B. Myrmecodomatia from the side x 1½.

(After Wheeler and Bequaert, 1929).

sacs, or pouches, produced by an evagination of the base of the leaf-blade towards the upper (dorsal) side of the leaf. They open on the under side of the leaf in the axil between the midrib and the next longitudinal vein.....In some species the pouches are still borne by the blade and are entirely or partly included in it; in others they are attached to the petiole, often at a considerable distance from the base of the blade, but even in these cases a hollow channel, running along the upper surface of the petiole, connects each sac with its opening, which is still situated in the axil of the midrib on the underside of the leaf.

Since the pouches are simple evaginations of the leaf blade they are naturally hollow, and the ants have nothing whatsoever to do either with their production or with the formation of their opening. There is not the slightest possibility that they can be galls, since they are produced with their usual size and shape even in seedlings which have never been attacked by the insects. They are inherited structures and, moreover, their shape and position are characteristic of the several species. That they owe their origin to acarodomatia which for some obscure reason becomes enormously enlarged, is a fanciful hypothesis which it seems impossible either to substantiate or to disprove with any facts." (Fig. 7)

In the same paper it is stated that coccids are occasionally found in the pouches; it is also indicated that the guest ants

provide little or no protection for the foliage.

Melin (1930) made a careful statistical investigation of the amount of damage done by phytophagous insects and caterpillars. For this purpose he studied one bush at a time and, distinguishing between the leaves with sacs and those without, made a record of the numbers of intact leaves and those gnawed by ants. Those in the latter category he subdivided according to the extent of the damage, designating them as follows:

I: slight traces of gnawing.

II: big or numerous holes.

III: leaves with laminae reduced by half or more.

It is not possible to quote his statistics in full, but the following shows the results for an average Tococa bush in which the pouches were inhabited by a species of Crematogaster.

Leaves	No.	No. intact	Nos. of bitten leaves.		
			I	II	III
with sacs	165	8	39	86	32
without sacs	65	4	14	36	11
Total	230	12	53	122	43

Thus, on this inhabited tree, 95% of the leaves were damaged, while there is no significant difference between the leaves with and those without sacs. The sacs themselves were sometimes partly destroyed.

From this and the other trees examined Melin concludes:

"Even if the inadequacy of the material does not admit of any safe conclusions as to the correlation between the sacs and the bites, my observations at any rate clearly indicate that the ants hardly protect the Melastomae against phytophagous enemies."

He performed further experiments in which he placed an ant of an Atta species on an inhabited Tococa leaf under various circumstances. In 9 out of 11 cases he observed no hostile reactions from the obligatory ants. This evidence, however, must be considered to be of little value, because it is impossible to argue from experiments with an individual ant how the obligatory inhabitants will react to an invasion by a whole host of their leaf-cutting relatives.

Melin's statistics, however, make it quite clear that Schumann's (1888) assumption, that myrmecophytic Melastomae are protected by their ants, is not justified by the facts of the case.

DISCHIDIA.

This genus includes some 50 species all of which are climbing epiphytes with slender liana-like stems straggling over the branches and twigs on which they grow. A few of these species are associated with ants. The normal leaves are fleshy, kidney-shaped organs, concave on the under side. Adventitious roots spring from a point near the petiole and shelter between the leaf and the bark of the tree on which the plant grows. The species associated with ants present, in addition, cone or pitcher shaped leaves in which

the ants are found. These pitchers take different forms, of which the main types are represented by the two species, D. Rafflesiana Wallich and D. Shelfordii Pearson; most of the published observations were made on these plants.

Dischidia Rafflesiana.

The pitcher shaped leaves are found mainly on the older part of the plant. The pitcher develops by the bending of the apex of the leaf towards the base. This is brought about by the arrest of the apical growth of the leaf, followed by a rapid growth of the central portion. These hollow pitchers are filled with adventitious rootlets which enter by the opening at the base. About the rootlets are fragments of soil and leaf detritus, and the whole is usually swarming with ants, which sometimes make regular nests in the pitchers. The inhabiting ant is usually Crematogaster (Ridley, 1910; Shelford, 1916; Bequaert, 1922).

There is little agreement as to the true function of these pitchers. Delpino and others have suggested that the plant is carnivorous and that the pitchers, like those of Nepenthes, catch insects which are drowned in the water contained in them. Treub rejected this view on the evidence that though the pitchers were, in the wet season, more or less full of water they contained only a very few drowned insects. Ridley (1910) refuted the theory on the ground that "only a very few pitchers ever contain more than a drop or two of water, and insects do not appear to enter those

that do." Delpino's suggestion has received very little support, as has also the hypothesis that the pitchers are water-vessels supplying rain water to the roots. Beccari regards the pitchers as comparable to galls, and developing only after a stimulus from the ants. This has been disproved by the development of normal pitchers where ants had no access to the plants. Treub regards the pitchers as part of the normal development of the plant and adapted purely and simply to the purpose of protecting the rootlets. Shelford (1916) supports this view, pointing out also that the pitchers cannot be regarded as absorbent organs since both inner and outer surfaces are coated with wax.

Beccari and others regarded the plant as being truly myrmecophilous. Treub held that the ants, far from being of use to the plant, are actually harmful because they nibble the rootlets. Ridley (1910) concludes that the ants are merely collecting the wax on the walls or else are facultative guests; Shelford (1916) believes that the association of the ants with the plants "has played at least a small part in the development of the pitchers."

If the ants serve any purpose to the plant it must be by the supplying of food in the form of nest-débris to the rootlets enclosed in the pitchers. No insects attack the plant, so that no guard is needed. Ridley (1910) asserts that untenanted plants seem no less flourishing than those inhabited by ants.

Dischidia Shelfordii.

In this species the pitchers are double, a small one being

found inside each large one. The inner pitcher is formed by the inflexed margin of the outer pitcher; the infolding takes place in the funnel-shaped depression opposite to the insertion of the petiole. Its walls are thickly beset with small glandular hairs. In the large outer pitchers rootlets, particles of soil and also numbers of ants are found. Microscopic examination of the inner surface of this outer pitcher reveals the presence of a "dense waft of superficial mycelium" which grows from definite centres or rosettes. In one species there were found in the inner pitchers small irregularly shaped masses sweet to the taste. (Pearson, 1902; Shelford, 1916; Bequaert, 1922).

Pearson regarded the sweet bodies as decomposition products resulting from punctures made by the ants. He suggested that the inner pitchers serve as harbours of refuge for the ants when the outer pitchers become nearly filled with rain. Shelford expresses the conviction that the inner pitchers will eventually be shown to be "designed for the purpose of producing a food substance attractive to the ants". He concludes therefore that these double pitchers are developed with a double purpose - to store water and protect rootlets, and to attract and shelter ants. He implies the belief that Dischidia Shelfordii is truly myrmecophilous.

CORDIA.

The genus Cordia Linnaeus is represented in the tropical regions of both hemispheres, but the few of its 250 species which

are true myrmecophytes seem to be confined to South America. The myrmecophytic species belong to two sections, the Physocladae and the Gerascanthi: recent work by Bailey (1924) has revealed the fact, not previously fully realised, that it is important that the representatives of these two sections should be considered separately as far as myrmecophytism is concerned. The Physocladae include -

Cordia nodosa Lamarck.	Brazil.
C. miranda de Candolle.	Brazil.
C. hispidissima de Candolle.	Brazil.

The Gerascanthi include -

C. Gerascanthos Jacquin.	Central and South America.
C. longituba Chodat and Vischer.	Paraguay.

C. nodosa, which Schimper encountered in Pernambuco, is the most famous of the above species. Most of the published observations are concerned with it, and it may be taken, for the present purposes, as typical of the Physocladae.

Morphology.

Physocladae.

The morphology of the species in this section is of special interest, because the myrmecodomatia differ so remarkably from the nodal or internodal swellings of other tropical myrmecophytes. The following description of C. nodosa is from Bailey (1924).

"The large leaves which, like the stem, are provided with long reddish hairs, are alternate, paired, or grouped in

Fig. 8. Cordia nodosa Lamarck.

False whorl with inflorescence, axis and lateral swelling. One-half natural size.

(After Schimper, 1888).

false verticils of four. The subnodal portion of the stem, subtending each verticil of leaves, is strongly thickened and angular, and usually (although not invariably) is provided with a long bladder-like swelling. This pouch is jacketed internally as well as externally by a cuticularised epidermis and numerous trichomes. It subtends the lowest of the four leaves, in the axil of which is a small apical outlet which is not excavated by the ants. Above this leaf the ~~is~~ thickened and much compressed primary axis ~~which~~ gives rise to lateral inflorescences which are inserted in the axils of the three remaining leaves." (Fig. 8.)

There have been several theories about the mode of origin of the hypertrophy. Schimper (1888) believed that it is formed by the enlargement of the base of the petiole of the lowest leaf. This petiole he supposed to be adnate to the compressed portion of the main axis. Schumann (1888) opposed this view. He argued that the bladder like swellings are cauline, rather than adnate foliar structures and that the inflorescences are terminal. He based his conclusions on analogies with the myrmecodomatia of Duroia hirsuta and various Gerascanthi. Mez (1890), while agreeing with Schumann that the inflorescences are terminal, inferred that the cavities are formed by lateral invaginations. He believed that these invaginations were originated by insects which lived in the lateral grooves, but that they subsequently became accentuated and inherited as adaptations for housing ants: during

the phylogenetic development of the myrmecodomatia the margins of the cleft formed by the invagination fused together and isolated the internal layer of epidermal tissue.

Bailey (1924) has disproved this theory; examining examples of Cordia from the Kartabo region of British Guiana, he was led to different conclusions. From a close histological examination of the structure of the domatia he describes its walls as consisting of eleven layers (1) outer epidermis, (2) cortical parenchyma, (3) sclerenchyma, (4) phloem, (5) xylem, (6) medullary parenchyma, (7) xylem, (8) phloem, (9) schlerenchyma, (10) cortical parenchyma, (11) inner epidermis. Horizontal sections showed no connections between the rings of homologous tissue. The inner fibrovascular cylinder was found to be more or less rudimentary.

From serial sections he derived the following description of the morphology of the domatium:

"Below the subnodal hypertrophy, the stem is of normal structure. Above this level it rapidly increases its growth. As it does so, the circumference of its concentric layers of epidermal, cortical, and fibrovascular tissues become correspondingly enlarged, and a commodious internal cavity is concomitantly formed in the dilated core of medullary parenchyma. This chamber, unlike that of the caulinary domatium of other myrmecophytes, is characterised by being jacketed by centripetal layers of epidermal, cortical and more or less

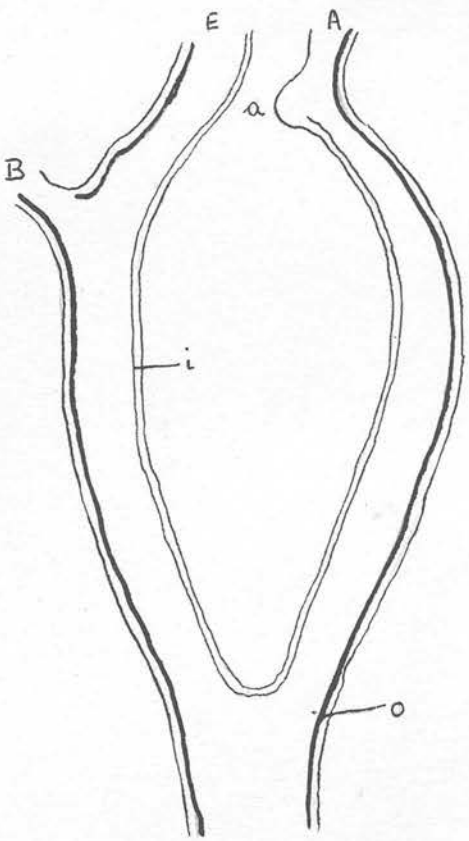

Fig. 9. Cordia nodosa Lam.

Diagram of longitudinal section of myrmecodomatium, showing centrifugal (o) and centripetal (i) fibrovascular tissues: a, entrance aperture in axil of leaf (A); E, terminal inflorescence.

(After Bailey, 1924).

rudimentary fibrovascular tissues. In other words, there is no indication of a compressed stem and adnate petiolar enlargement, nor of an extensive lateral invagination. The centripetal layers of epidermal, cortical, and fibrovascular tissues unite with the homologous centrifugal layers only in the apical portion of the wall of the domatium which surrounds the small circular aperture." (Fig. 9)

From the above evidence Bailey is led to reject the explanations given by Schimper, Schumann and Mez as being inadequate mainly in respect of development ontogenetic and phylogenetic. He himself concludes that the invagination originates, not in a longitudinal groove, but in the axil of one of the leaves of the pseudo-apical verticil. The development of this invagination produces an elongate-saccate ingrowth of the epidermal, cortical and fibrovascular tissues into the rapidly enlarging core of medullary parenchyma. He suggests that it may be inferred, from the absence of a rudimentary bud in the axil of a leaf which subtends an entrance aperture, that this growing point may be concerned in the formation of the invagination.

He infers also that the cauline axis usually terminates in an inflorescence, while the buds in the axils of three of the leaves of the false verticil of four usually give rise to one or more lateral axes of vegetative elongation.

Gerascanthi.

In external appearance there is little difference between

the Physocladae and Gerascanthi, but morphologically the domatia are fundamentally different. In the latter the domatia "are irregularly shaped hypertrophies of the axis of the large diffuse inflorescences, or of the transitional region between cauline and floral axes." (Bailey 1924). They are not jacketed internally by invaginated layers of epidermal, cortical and fibrovascular tistues, and the apertures are not preformed, but are excavated by insects on the sides of the hypertrophy. (Spruce 1908; Bequaert, 1922; Bailey, 1924).

It is therefore clear that these structures are quite different morphologically from the domatia of the Physocladae. They resemble rather those of Cuviera, Cecropia and Plectronia.

Ecology.

Several kinds of ants have been found in the cavities in Cordiae, e.g. Azteca, Pseudomyrma, Allomerus and Cryptocerus.

Schimper (1888), Schumann (1888), Beccari and Spruce (1908) considered the peculiarities of structure in the Cordiae to be hereditary malformations in adaptation to the ants. Spruce points out that communication between the domatia is maintained, sometimes by the hollowed interior of the branches, but nearly always by a covered way along their outside. Mez (1890), as has already been stated, regarded the cavities as lateral invaginations, and thought that they were a kind of insect gall which had become inheritable. Buscaloni and Huber (1900) developed the suggestion made by Spruce that the ants retreat to the bushes to escape from

inundations. Rettig (1904), Ule (1906) and others questioned the possibility of the domatia being adaptations to ants but offered no alternative explanation of their occurrence.

Chodat and Carisso (1920) formulated "Une nouvelle théorie de la myrmécophile". They contend that the domatia originate as insect-galls, basing their conclusion on the fact that they found eggs and larvae of hymenopterous parasites in immature myrmecodomatia of Cordia glabrata, C. alliodora, C. Gerascanthus, C. Gerascanthoides.

Bailey (1924) points out that the mere fact that gall-insects are found in the hypertrophied structures does not prove that these are traumatic in origin. They may be inherited peculiarities merely used by the insects as suitable places for oviposition. Bailey was the first author fully to realise the necessity of distinguishing between Physocladae and Gerascanthi, and therefore the danger of applying to all Cordiae conclusions drawn from species of only one section. He finds in fact that the circumstances are quite different for the two sections.

With respect to the Physocladae he concludes that the myrmecodomatia are formed by neither ants nor gall-insects, nor modified by gall-insects before being inhabited by ants.

In the case of the Gerascanthi owing to the irregular shape and more or less sporadic distribution of the cauline hypertrophies, he concludes differently:- "if the myrmecodomatia are not actually originated by gall-insects, they may be considerably

accentuated by them."

In both cases he believes that the ants are parasites, taking full advantage of the structural peculiarities of the plants without rendering any service in return.

Coccids.

Coccids are generally but not always found in the domatia of Cordiae. The ants, however, do not excavate pit- or groove-like depressions in the walls as in Cecropia, Tachigalia, etc. Bailey suggests that this may be due to the fact that there is no necessity to expose soft tissues for the mouth pieces of the coccids: in the myrmecodomatia of Cordia as in the sacs of Tococa the softer and more nutritious tissues are not completely isolated from the chambers. In Cecropia, Cuviera, Plectronia, etc., on the other hand, where the coccids lie in pits or grooves, a jacket of thick walled cells separates the soft tissues from the internal cavity.

There appears to be little or no evidence to support the assumption, inherent in the hypothesis of those who support the theory of myrmecophily, that the species of Cordia are protected against phytophagous enemies by the inhabiting ants.

CLERODENDRON.

This is a large genus whose 200 odd species are distributed between the tropics in the Old World. A number of species have been found associated with ants but the evidence is too fragmentary to show whether any of these are true myrmecophytes. This is made

the more doubtful by the fact that Bequaert (1922), on making a systematic study of Clerodendron formicarum Guerke, found its supposed myrmecodomatia to be true insect galls. That this is so is, in his opinion, indicated by the irregular distribution of the swellings, their typical gall-like structures, and the fact that he always found an insect larva in the young galls.

It is possible, however, that C. myrmecophilum Ridley, C. breviflos Ridley, C. fistulosum Beccari, and some others may be true myrmecophytes. These have hollow stems and are usually unswollen, though Beccari described them as having swollen internodes. The ants gain entrance by gnawing apertures below the insertions of the leaves. These spots are very constant in position and before being attacked are marked by a little circular patch of a texture and structure different from that of the surrounding parts.

The leaves are in pairs so that there are usually two apertures in each internode, but there may be one or none. Shelford states that the internodal cavities never communicate with each other internally, but are always separated by thick partitions. Blatter (1928) mentions the fact that the lower surfaces of the leaves of C. fistulosium bear nectaries. (Beccari, 1904; Ridley, 1910; Shelford, 1916; Blatter, 1928; Bequaert, 1922).

Beccari suggests that the hollowing of the stem by the ants serves to strengthen it. This is improbable, and in any case the pith probably dries up of its own accord as in so many other

myrmecophytes. No other advantage to the plant has been suggested. Ridley (1910) states that the plant does not suffer from the absence of the ants.

VITEX.

The genus Vitex Linnaeus contains over 100 species and is distributed over the tropical and subtropical parts of both hemispheres. The plants are usually creepers and are closely allied to Clerodendron. Only two species are definitely known to be myrmecophytic: Vitex Staudtii Guerke, and V. yaundensis Guerke. It is quite probable, however, that other tropical species are associated with ants. The following descriptions apply to Vitex Staudtii but, in respect of their relations to ants, there is no important difference between the two species.

Vitex Staudtii. Morphology.

This plant is usually found growing in very moist places. Its stem and branches are glabrous and are sharply quadrangular; except in very young plants they are hollow. The phyllotaxy is decussate, i.e. pairs of opposite leaves alternate with each other at right angles, resulting in four vertical rows of leaves. At each node, on opposite sides of the stem and midway between the two leaf scars, are located the entrance apertures to the hollow interior. Corresponding to the decussate phyllotaxy of the plant these are found on the alternate sides on the next node. The quadrangular shape is more marked on the younger branches: there

are usually no swellings on either stem or branches.

In adult and colonised plants the entrance apertures lead into a cavity which is continuous nearly from top to bottom of the plant; all the internodes and branches communicate with one another freely. The ants have cleaned out most of the medullary tissue from the side walls of the cavity, but they leave a layer of it for a short distance a little above each node. The constriction so formed probably serves to keep the ants in one internode from dropping down into the one below. It also results in the apertures being located near the top of each subdivision of the cavity - a circumstance which would appear from other cases to be preferable to the ants.

The inner walls of the domatia also exhibit a series of depressions, known as lateral cavities, arranged in two longitudinal rows. These two rows are opposite each other and in each internode they subtend the apertures of the node above. Their position therefore changes at every node. They are arranged at irregular intervals and the number in a single row may reach 50, but is usually less. No analogous pits or depressions have been observed in any other myrmecophyte. They differ from the depressions in Cuviera, Cecropia, etc., in that they are much deeper. They perforate the xylem and end blindly just under the cambium, where the end of the cavity is filled up by a cap of sclerenchymatous tissue

The entrance apertures resemble the lateral cavities in their

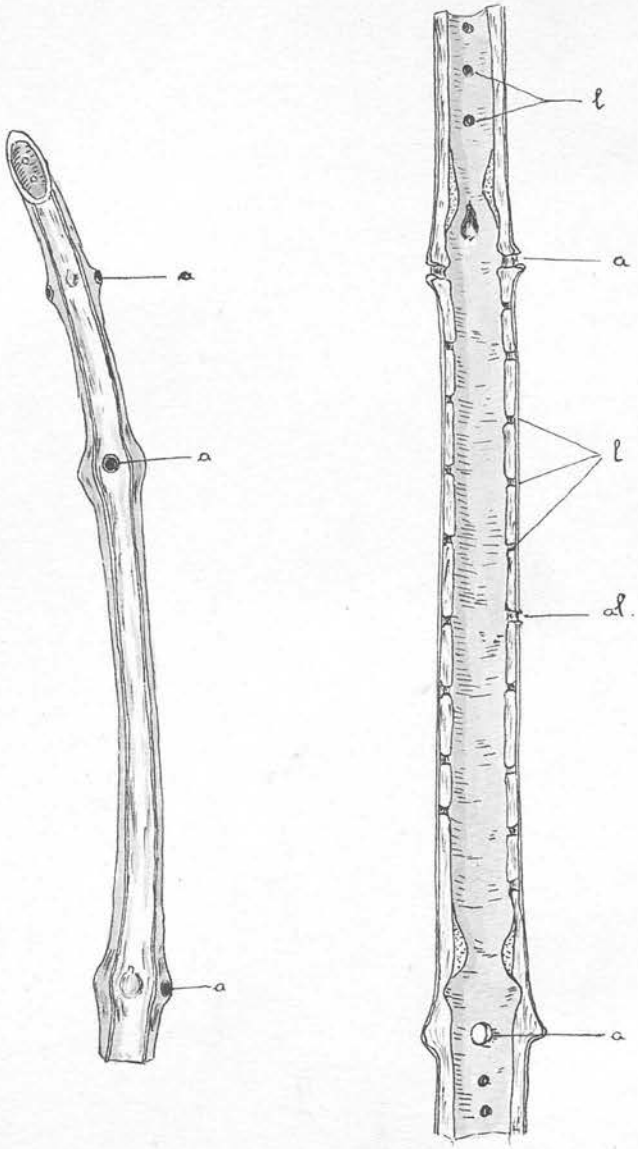

Fig. 10. Vitex Standtii Guerke.

A. External view of portion of stem inhabited by the ant Viticicola tessmanni.

B. Longitudinal section of older stem.
a. entrance to cavities at nodes.
b. lateral cavities excavated by ants through the xylem and ending blindly beneath the bark.
al. accessory exit where one of the lateral cavities was gnawed through the bark.
(After Bequaert 1922).

nner portions. In the outer portion is found a ring of sclerenchyma (c.f. cap of sclerenchyma in lateral cavity) which projects slightly on the outside of the stem, producing a crater-like appearance. This sclerenchymatous ring prevents the cambium and cortex from forming lateral callus which would seal the exit hole as happens in other myrmecophytes). It occasionally happens that one of the lateral galleries pierces the cambium, cortex and bark. The disk of sclerenchyma is then replaced by a projecting sclerenchymatous ring similar in all respects to that found on the apertures at the nodes. (Fig. 10).

Origin of Apertures and Cavities.

Examination of a young specimen of Vitex Staudtii still free from ants reveals no depression, elevation or scar on the surface to indicate the points where the entrance holes would later be excavated. Histological study, however, shows that the most favourable situation for the nodal apertures is midway between the point of attachment of the leaves. At this point, owing to the concentration of conducting tissue in the leaf traces, there is a comparative absence of these vessels. How the ants locate the spot is still a mystery (vide infra).

The stems of young seedling plants, which are not inhabited by ants, are filled with medullary tissue: those of inhabited plants are hollow except in the vicinity of the growing points. While these facts suggest that the central cavities are excavated by the

ants, yet the evidence is purely circumstantial. Analogy with other myrmecophytes, comparison with non-myrmecophytic representatives of the genus Vitex, and histological evidence suggest that there is an inherent tendency towards the formation of hollow stems and branches. The ants may, however, accelerate the formation of the central cavities.

In considering the lateral cavities the most obvious point is the close correlation between the distribution of these cavities and the phyllotaxy of the plant. No trace of them is found in young internodes where the pith has not yet been removed by the ants. They are not natural gaps in the woody portions of the wall but are excavated by the ants in peculiar cores of delicate, unlignified cells, that are symmetrically distributed in certain radii of the stem, and surrounded by abnormal tissues similar to those presented by heteroplasmatic zoocecidia. The arrangement of these galleries in two rows below the aperture of the upper node is due to the fact that the ants avoid the other sides of the stele because they contain the great majority of the conducting vessels. These are collecting to pass out to the leaves at the next node. The lateral cavities are excavated in those portions of the xylem which are devoid even of a narrow fringe of small primary tracheae.

It was at first believed that the galleries assisted in the aëration of the hollow interior: this is disproved by the fact that the bark is impenetrable lateral to the cavities: the

presence of the cap of sclerenchyma adds to the impossibility of such a function. They are not used by the ants for their eggs or very young larvae; and that they do not correspond to the depressions for coccids in other myrmecophytes is clear from the fact that coccids are never found in the domatia of Vitex Staudtii. They seem to serve as a source of food for the ants.

The Ants.

Adult plants of Vitex Staudtii are always inhabited by ants, which are invariably of the species Viticicola tessmannii (Stitz). These red ants are exceedingly vicious and alert, with a very painful sting. They constitute a very efficient bodyguard for the host plant, yet galls have on occasion been observed on the leaves of an inhabited plant.

The entire plant shelters one ant community containing, in addition to one or more dealated queens, a number of fertile, ergatoid, wingless females. The ants appear to remain, at least in the daytime, within the domatia, and are modified to their life in the dark. It would appear that they never leave the host plant because a) the plant always grows in swampy places, and b) examination of the food pellets dissected from the infrabuccal pockets of the adults and the trophothylaxes of the larvae has failed to reveal traces of food from an outside source.

The ants appear to find their necessary nourishment by eating, and feeding to their larvae, some of the less vigorous

progeny; from the medullary tissue of young twigs; but mainly from a layer of nutritive tissue which is found on the sides of the lateral cavities. That these heteroplasias provide the principal food of Viticicola tessmanni is suggested by the following facts -

(1) Field observations have failed to reveal an external food supply.

(2) The pellets (from infra-buccal pockets) do not contain food from an outside source.

(3) The myrmecodomatia do not contain coccids.

(4) The starch-containing tissues are not excavated extensively by the ants.

(5) The heteroplasias are traumatic structures produced by the ants.

(6) They resemble gall-heteroplasias and have a protein-fat layer which is gnawed by the ants.

(7) The pellets in the larval trophothylaces are composed of fragments of this tissue and bits of ant larvae or triturated eggs.

The foregoing account of the morphology and ecology of Vitex Staudtii is based on the descriptions given by Bailey (1922 a.) and Bequaert (1922).

MYRMECODIA and HYDNOPHYTUM.

The family Rubiaceae, to which the genera Myrmecodia Jack and Hydnophytum Jack belong, contains by far the largest number of myrmecophytes.

Myrmecodia and Hydnophytum, including respectively 18 and

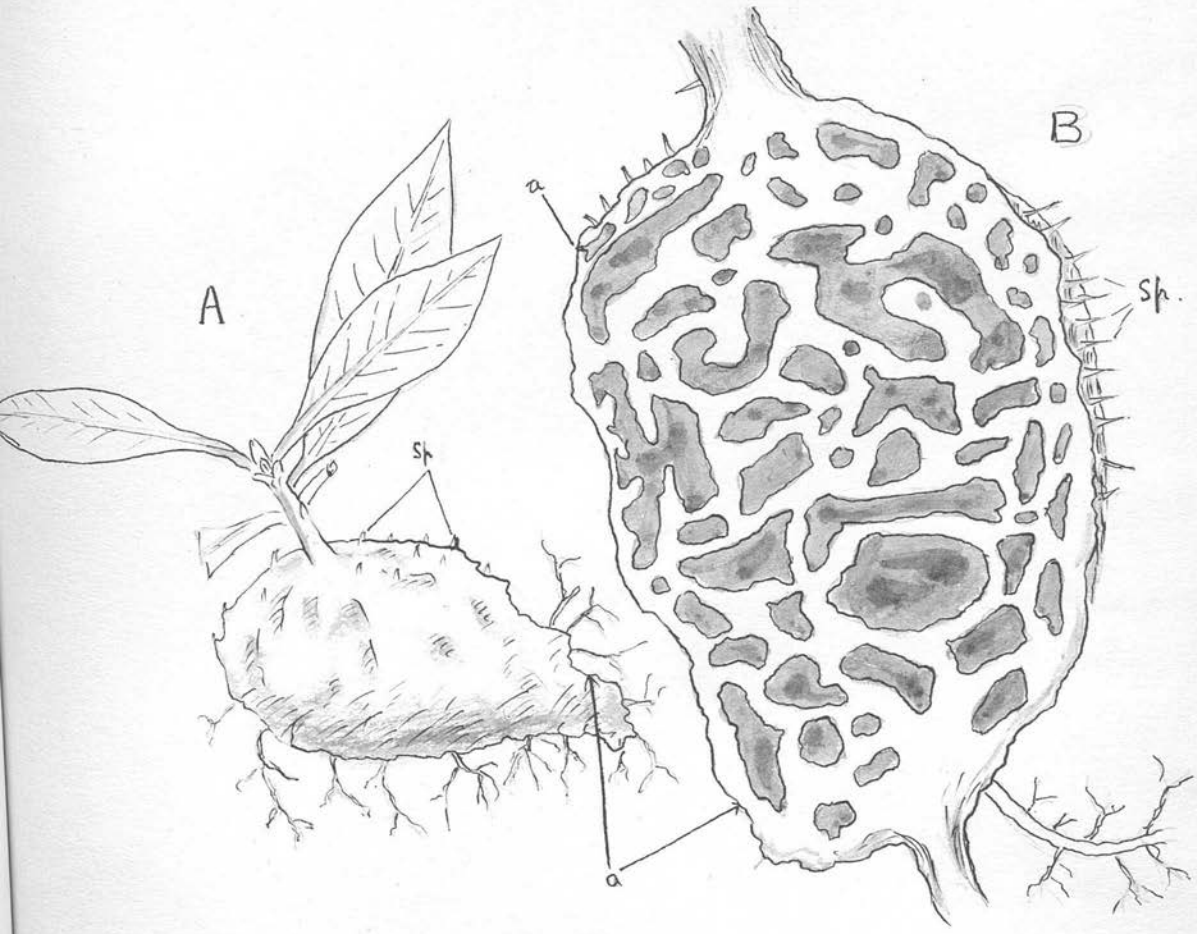

Fig. 11. Myrmecodia echinata Jack.

A. Young plant.

B. Longitudinal section of swollen rhizome showing galleries, aperatures (a) and spines (sp).

(After Treub, 1883).

35 species, present similar characteristics especially in respect of their myrmecophytic characteristics. They are epiphytes and occur in the oriental region; they grow in the dense crowns of trees but not as true parasites like mistletoe. Most of the published accounts have reference to various species of Myrmecodia of which the most famous are M. armata de Candolle, and M. tuberosa Jack. Of Hydnophytum the best known species is H. montanum Blume (= H. formicarum Beccari).

The plants are characterised by the fact that the rhizome or hypocotyl is swollen into a basal pseudobulb or tuber. The tuber of an adult specimen of M. tuberosa measures about 30 centimetres in length by 20 in diameter; its surface is ridged and on the ridges are sharp spines. There also grow from the tuber numerous rootlets by means of which the plant is attached to the bough on which it lives. The rootlets and the spines are homologous structures. The tuber itself is tunnelled by an elaborate system of anastomosing cavities which communicate with the exterior by means of numerous pores, the larger of which are situated at the base of the rootlets (Fig. 11). The walls of the galleries are of two kinds: a) smooth and light brown in colour, and b) blackish and covered with small pimples. The species of Hydnophytum have large tubers, galleried in the same way, but spineless; the leaves of this genus are much more fleshy than those of Myrmecodia. The galleries are almost invariably found to be inhabited by ants, generally Iridomyrmex, and less often Crematogaster.

Myrmecodia and Hydnophytum are among the most famous of all myrmecophytes, and a considerable amount of attention has been paid to them by various students of myrmecophytism. The result of their investigations will be stated by summarising their work in chronological order.

Rumphius in 1750 first discovered these remarkable Rubiaceae with ant-tubers. He believed that the ants not only lived in the galleries but actually produced the vegetable tissue. Jack (1825), however, dispelled these curious ideas; he distinguished between Myrmecodia and Hydnophytum and wrote of the latter: "The tuber is generally inhabited by ants, and hollowed out by them into numerous winding passages."

In 1882 Treub published a paper in which he professed to show that the galleries and the entrance apertures were formed without the intervention of the ants; and also that the adult plants continued to flourish although completely abandoned by the ants. These facts he demonstrated by growing plants to which no ants had access. At the same time he was careful not to deny that the ants may serve some useful purpose to the plants: he suggests the following services, each with considerable doubt - a) the ants may remove débris in the form of dried tissue from the galleries; b) they may act as a defensive army; c) they may fertilise the flowers; and d) they may assist in transporting the seeds. He expressed the opinion that the purpose of the galleries is "à per-

mettre une circulation libre de l'air atmosphérique au dedans du tubercule", and regarded the prominences on their walls as lenticels.

Beccari, in Malesia II (published in 1884), opposed this view. In spite of Treub's evidence he held that the ants excavated the cavities in the swollen rhizome; that it was impossible for the young plants to develop without the intervention of these insects; that their activity in excavating caused the tuber to grow enormously, while its weight was not proportionately increased; and that the galleries thus increase the absorbent surface of the rhizomes.

Treub started another series of experiments to confute Beccari's ingenious arguments, and published the results in 1888. He had raised Myrmecodia both from seed and from young plants in the complete absence of ants and always obtained healthy adult plants with galleried tubers. He therefore concluded -

> "Pas plus que pour la croissance de Myrmecodiae plus âgés, la présence de fourmis n'est nécessaire au développement des plantules. Leurs tubercules croissent, les orifices prennent naissance et les feuilles se montrent hors de toute action possible de fourmis."

He inferred, therefore, that none of the peculiarities of the plant could be considered as adaptations to ants. He modified his original view as to the function of the galleries by stating

that these are protective devices against drought; they store water and reduce transpiration to a minimum. Finally he concludes that the ants must be regarded as mere opportunists who take advantage of the shelter afforded by the plant but offer no service in return. The relationship, that is to say, is one of parasitism and not symbiosis.

That Beccari was partly convinced by this new evidence is clear from a later publication (1904). There he admitted that the swelling is not due to the ants. He clung to the idea, however, that the galleries, and especially the apertures, are not normal. His observation that the ants help to make the galleries is of little value. He believed that the tuber acts as a water reservoir. The ants, he said, defend the plant, and may also benefit it by accumulating in the galleries detritus, excreta and humus which may be utilised by the plant for alimentary purposes. He suggested, accordingly, that the papillae "are more probably subsidiary organs of alimentation". Finally, he admitted that the tubers may have originated through physiological causes, but insisted that the ants have assisted in their phylogenetic development, and that the relation between ant and plant is now symbiotic.

While this controversy was going on Forbes (1880 and 1885) contributed evidence that the tuber, galleries and apertures develop normally in the absence of ants. Karsten in 1895 also denied the supposed symbiotic relationship between the Myrmecodiae and ants. He believes, however, that the cavities, in addi-

tion to their respiratory and water absorbing functions, also assimilate certain dissolved nutritive elements introduced by the ants or found in the excrement of these insects.

Rettig (1904) showed experimentally that rain water could be absorbed by the tubers. At the same time he emphasised the importance of the galleries in aërating the tuber, by noting that these epiphytes grow high up in the trees where they are exposed to the full heat of the sun. Wallace, in the notes which he added as editor to Spruce's work (1908), expressed the opinion that the ants were attracted to the plant both by the pith (as a source of food) and a watery fluid secreted in a large central chamber.

In 1911 Miehe published a valuable contribution to our knowledge of the Myrmecodiae. According to his findings the inner walls of the cavities of M. tuberosa are, as a rule, clean; those in certain portions are smooth, of a brownish-yellow colour, never covered with fungi, and the pupae of the ants are always kept in such galleries only; others are blackish, strewn with paler papillae, the dark colour 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 odour. It is evident that the tips of the hyphae are cut off by the ants and in some places whole sods of those filaments are trimmed evenly, yet Miche believes that the insects do not feed on the fungus, but merely cut the hyphae 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 papillae are evidently not rudimentary roots or root-buds; 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.

Shelford (1916) tries "to steer a middle course" between Beccari and Treub. This amounts to admitting that the peculiar structure of this plant is an adaptation to ants, with the qualification that the relation is none the less not symbiotic because the ants serve no useful purpose to the plants. Blatter (1920) believes that the plant derives benefit from the deposition of excrements in the galleries, but can see no evidence of original adaptations to visiting ants.

There can be little doubt that the great weight of the evidence is in favour of a non-symbiotic relationship, or at least that the upholders of myrmecophily have failed, as yet, to demonstrate that in respect of Myrmecodiae the plant derives any benefit from the ant.

The work of Treub (1888) and Miehe (1911) is of interest in that, both in the thoroughness of their investigations and the

nature of their conclusions, they stand as forerunners of the modern critical experimental attitude in research in myrmecophytism, which has been most in evidence in America in the last twelve years.

DUROIA.

The genus Duroia Linnaeus fil. is confined to tropical South America. Four of its ten species are known to be myrmecophytic.

Three of these present branches with spindle-shaped, hollow swellings which are inhabited by ants (Schumann 1888). Schimper (1898) believed that not only the opening but also the hollow chamber in the stem had arisen as an adaptation to ants. He points out that since the cavities are present in some only of the internodes, and since only the upper half of an inhabited internode is hollow, the principle of providing resistance to bending is no longer applicable. Spruce (1908) also refers to these species as being associated with ants.

The fourth species is Duroia saccifera Martius. It was described as a myrmecophyte by Schumann (1888) and Spruce (1908). The following account of the myrmecodomatia is from Wheeler and Bequaert (1929).

"The myrmecodomatia of D. saccifera are two pouches at the base of the leaf on each side of the petiole. These sacs are completely separated from each other by the whole width of the petiole on the upper as well as on the under side of

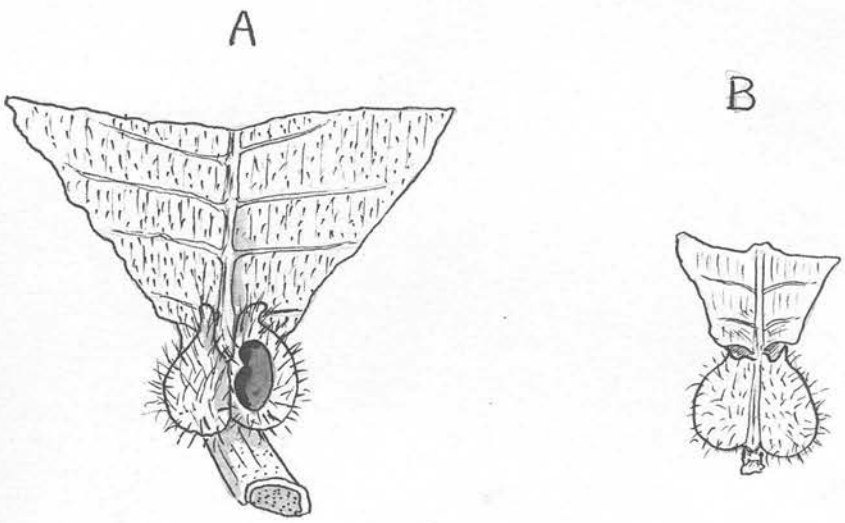

Fig. 12. Duroia saccifera Hook. fil.

A. Underside of leaf showing pair of pouches.

B. The pouches from above showing entrances to myrmecodomatia.

(After Schumann, 1888).

the leaf. They are nearly symmetrical, ovate, 10 to 14 m.m. long, 6 to 7 m.m. wide and 4 to 6 m.m. thick, and are completely closed at the lower end and along the petiole, but open at the upper end by a narrow slit in the deep sinuous notch which divides the base of the leaf from the pouch (Fig. 12). The pouches might be regarded as having been formed by the recurving of the decurrent bases of the blade to the upper side of the leaf, and the growing fast of the free edges of the recurved portion to the petiole....Both the inner and outer surfaces are densely covered with long, hispid hairs. Those of the inner surface converge towards the upper slit, which they partly close up."

Ants are almost invariably found in these domatia. They are usually Solenopsis, Brachymyrmex or Azteca, but Üle (1906) records finding Allomerus. Spruce and Schumann assumed that the ants protect the plant against phytophagous enemies but Wheeler and Bequaert record finding the leaves of inhabited plants to be badly damaged by Attine ants and caterpillars.

PLECTRONIA.

Three species of this genus have been recorded as myrmecophytes. Bequaert (1922) describes in addition the myrmecodomatia of three unidentified species of Plectronia. In these myrmecophytes the domatia take slightly different forms. The following account applies to Plectronia Laurentii De Wildeman.

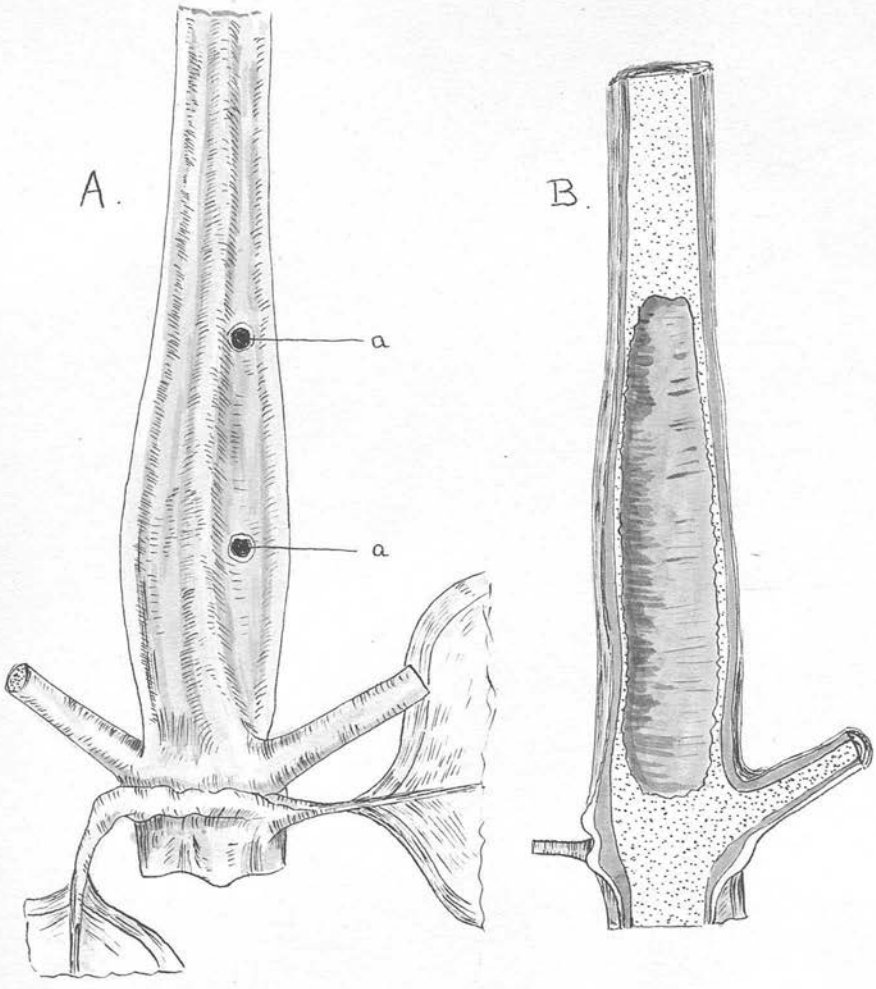

Fig. 13. Plectronia Laurentii De Wildeman.

A. Portion of branch with swelling above node inhabited by ants, showing aperatures (a) to the domatium.

B. Longitudinal section of the myrmecodomatium.

Natural size.

(After Bequaert, 1922).

Plectronia Laurentii is a bush or small tree with an erect, straight trunk bearing regularly opposite, nearly horizontal branches. The branches are strikingly quadrangular in shape. This squareness is shown most clearly on the young branches and is interrupted at the nodes only. The myrmecodomatia are located above the nodes; at these places there is a swelling with four broad flat sides. (Fig. 13)

In the older stalks the swellings are less marked but the myrmecodomatia are more extensive, even the partitions at the nodes being occasionally perforated. In younger branches the cavities are distinct and usually occupy the basal two thirds of each internode.

Two opposite sides of the domatia differ in thickness and in histological differentiation from the alternating pair. Entrance apertures and longitudinally arranged lateral excavations, which frequently coalesce to form grooves or trenches, are located in these walls, and change their position at each internode in correlation with the decussate phyllotaxy of the plant. The lateral cavities contain heteroplasias which resemble those of Vitex Staudtii in that their nutritive layers do not contain an amber-coloured substance. (Bequaert 1922 and Bailey 1922 a.)

The inhabiting ant is almost invariably a subspecies of Crematogaster africana, which Bequaert judges, none the less, to be a facultative guest. He and Bailey agree that the ants do not

excavate the cavity though they are responsible for the formation of the apertures and lateral cavities. The main cavity is formed through the drying up of the pith and the swellings are also normal structures. Coccids are usually found in the domatia; they are attached to the heteroplasias of the lateral pits by their sucking mouth parts, and are probably attended by the ants for the sake of their sugary excretions. Bailey also records the occurrence of "fungus-gardens" in a few of the specimens examined.

The other species of Plectronia resemble Plectronia Laurentii in all the main features: they have preformed, localized, hollow swellings of the branches, occupied by ants. They do not, however, have the peculiar quadrangular stems of the species described above.

CUVIERA.

The strictly African genus Cuviera de Candolle includes fourteen species of which the great majority are probably myrmecophytes. They are glabrous shrubs or small trees. The myrmecodomatia, as first pointed out by Schumann (1891) take the form of elongated, spindleshaped swellings on the branches. One or more apertures lead into the nodal domatia. The inhabiting ants are usually subspecies of Crematogaster africana.

Bequaert (1922) declares that the hollow swellings develop naturally, through the drying of the medullary tissue, and without the intervention of ants. It appears that the various ant colonies in a single Cuviera do not fuse into one great community as is the

case with the Pachysima of Barteria and the Viticicolae of Vitex Staudtii, yet they manage to live peacefully side by side. According to Bequaert the guest ants show no aggressiveness, remaining inside the domatia even when the plant was disturbed, with the result that leaves of a densely populated specimen may be badly eaten by caterpillars and insects.

Bailey (1922 a.) made a careful histological examination of two specimens of Cuviera. His observations confirmed the fact that the ants, or occasionally the larvae of certain beetles, occupy the hollow hypertrophies after they have become fully differentiated. The following is a summary of his findings.

The circular apertures are more or less symmetrically oriented in relation to the somewhat distorted - by torsion - decussate phyllotaxy of the plant, and shift their position regularly at each succeeding internode. The structure of the tissues surrounding the entrance holes indicates that the ants make the perforations subsequent to, or during the later stages of, the formation of the central cavities.

The myrmecodomatia of Cuviera are characterised by a number of elongated or oval pits which are located in the thinner sides of the branch. They are commonly occupied by coccids. They contain growths of thin-walled callus in which is found a golden yellow hyaline substance. The fact that the heteroplasias are absent from swellings which have not been occupied by insects shows that they are abnormalities produced by traumatic shock. Though the

sucking mouth parts of the coccids are embedded in the callus it is evident that the pits must have been excavated by the ants, because only the ants' strong mandibles could have made any impression on the tough and thick-walled cells of the medullary tissue in which the excavation was made. The ants as well as the coccids feed on the heteroplasias and these are found as usual whether coccids are present or not.

The walls of myrmecodomatia - in contrast with those of cavities without apertures - form the substratum for a more or less luxuriant growth of fungi. The hyphae are kept under control by the ants, and are usually found only at the two ends of the cavities where they ramify in a layer of detritus and penetrate the medullary tissue.

ANT-GARDENS.

The term "ant-gardens" or "flower-gardens" was first used by Üle (1901). It refers to a peculiar association, not uncommon in the tropics, between ants and certain epiphytes. Balls of earth and humus are found attached to the branches of trees and bristling with epiphytes in various stages of germination. The accumulation of the humus is helped by the roots of the plants. Their densely felted rootlets bind the soil particles together, and the whole ball is excavated to form galleries and chambers in which the ants live.

Üle first described these Ant-gardens in 1901. He distin-

guished between gardens inhabited by Camponotus and those inhabited by the smaller Aztecas. From the former he collected species of Philodendron, Anthurium, Streptocalyx, Aechmea, Peperomia, Codonanthe and Phyllocactus; from the latter species of Philodendron, Nidularium, Ficus, Marckea, Ectozoma, Codonanthe and Gesneriaceae. He inferred that "the ants sow and care for these plants, which would otherwise be unable to exist, but in return enable the ants to construct arboreal nests insured against being washed away by the torrential rains and protected from the scorching rays of the sun." He also claimed to have shown by experiment that the seeds of the epiphytes are collected by the ants.

In 1906 Massart expressed the opinion that these epiphytes are "domesticated" by the ants, and would die but for their care. Ridley (1910) describes the development of the ant-gardens in Singapore. Particles of soil and mosses collect in a crevice on a tree and the epiphytes commence to grow on the patch so formed. The ants bring up soil from the foot of the tree and fill up the spaces between the roots, thus constructing shelters in which they make their nests. The earth thus brought up supplies food to the plant and also serves to keep the roots cool and moist. Ridley considers, further, that the plants show no modification to the ants, but that "the nesting of the ants among the roots is distinctly advantageous, seedlings not infested by ants being weaker and suffering more from drought".

Üle (1906) repeated his earlier conclusions with even greater

emphasis on the fact that the ants deliberately carry the seeds of the epiphytes to new crevices and notches.

> "I have established the fact that ants transport the seeds of certain plants into the crevices and notches of trees and bushes or into nests of earth built in such places; then by bringing up more and more earth they help the growth of the plants, and thus secure increase in volume and in firmness for their domatium."

Wheeler (1921) objected strongly to Üle's conclusions, citing the above and other passages of his work as "a classical example of the uncritical mixtures of observation, inference, assertion and speculation, which abound in the work of observers in the tropics" - an outburst which may reasonably be directed against the majority of the early students of myrmecophytism. Wheeler points out that none of the ants found in ant gardens are obligatory guests, and that he has observed single ant epiphytes growing in crevices with no ants present. He concludes that the ants cannot be responsible, as Üle declares, for the dispersal of the seed for the following reasons: a) from the distribution of the ant-gardens; b) from the fact that colonies are often started by single queens at a time when there is no fruit on the epiphytes; c) from the size of the seeds - they are too large to be carried by the ants; d) from the fact that Üle's experimental results may be explained by the acquisitiveness of the ants, leading them to carry off all sorts of portable organic bodies. Finally, he declares

that there is no evidence to suggest that the ants actually cultivate the growing plants, and concludes that judgment must be suspended until the whole question has been more thoroughly investigated.

III. MYRMECOPHILY.

Comparison of the myrmecophytes described in the previous section reveals the fact that they have nothing in common except that they all conform to the definition of ant-plants. Some generalisation is possible, however, if separate consideration is given (a) to those cases in which the domatia are leaf structures, (b) to those cases in which the ants inhabit hollow rhizomes, and (c) to those cases in which the ants inhabit hollow stems and branches.

LEAF STRUCTURES.

A considerable variety of types of domatia is found on the leaves of various myrmecophytes. In Dischidia the whole leaf is modified into a pitcher shaped cone; in other cases such as Tococa only a small part of the leaf shows peculiar structure; in Tachigalia the petioles are swollen and hollow; etc. With these structures may be considered the inflated leaf-sheaths of Korthalsia and the modified stipules of Macaranga. All these myrmecodomatia may be considered as being of a primitive type. They are not much sought by the ants, probably because they do not offer sufficient solidity or permanency as shelters for formicaries.

In many respects, however, these structures are very important in a consideration of myrmecophily and myrmecophytism. They provide striking evidence of the fact that, in the tropics, ants will use as domatia almost anything which will shelter their eggs and larvae from the sun and the rain. Again from the very primitive nature of the myrmecodomatia we may expect these cases to throw some light on the problem of the development of myrmecophytism. It is possible that the case of Dischidia is particularly illuminating in this respect. The simple pitcher-shaped leaves of D. rafflesiana we may suppose to have been evolved to serve some physiological function (though what this function is has been a matter for much discussion - vide supra). The ants then found these pitchers, judged them to be serviceable shelters for their formicaries, and inhabited them. Their presence may have interfered with the performance of the function for which the pitcher was originally intended. The plant was faced with the problem of humouring the ants in such a way as to inhibit their interference with the performance of the function which the pitcher-shaped leaf subserved. To this end the double pitchers as in D. Shelfordii were evolved; the ants were still better served by the plants, and the plants succeed in preventing the ants from doing any serious damage. Such a hypothesis is, of course, very incomplete and very speculative; it would appear, however, to represent a sequence of events biologically much more probable than the sequence implied in the hypothesis that the inner pitcher of D.

Shelfordii et developed ontogenically as an adaptation for the attraction of ants which were to perform some service, very obscure so far as we can see, to the plant.

Or we may consider the evaginations of the leaf blade which form the leaf-pouches of Tococa. That these should have been developed for the sole purpose of attracting the ants seems highly improbable. The only service which the ants have been supposed to render to the plant is that of protection: that such protection is not in fact given has been proved by the statistical investigations of Melin (1930). It would appear to be a much more reasonable hypothesis that the leaf pouches developed originally to subserve some function which we do not now appreciate; and that the ants found and utilised the domatia so formed. What, we may ask, would the plant do in such a circumstance? If the pouches could continue to serve their true function while harbouring the ants they would persist. Even if the ants made performance of that function impossible it would seem biologically improbable that the pouches should cease to be formed; as soon as they ceased to be inhabited by ants the old stimulus to formation might recur. In either case the present state of affairs is explained without recourse to the daring hypothesis of the protagonists of myrmecophily.

The ochreae of Korthalsia may be explained in the same way as the simple pitchers of Dischidia - the ants have found and used as a shelter a structure developed for a quite different purpose.

The hollow petioles of Tachigalia are of special interest since they suggest a transition to the hollow branches of Cecropia, Cordia, etc. Bailey (1923) expressed the opinion that these structures were developed normally for bio-physical reasons - "as being the method of producing the greatest resistance to bending with the least expenditure of material". It is not to be wondered at that ants should find this cavity and appropriate it for their own purposes. They excavate entrance apertures and make their nests inside the domatia. It is surely quite unnecessary to suppose that the domatium was formed for their benefit. And so long as their activity does not injure or kill the leaf, there would seem to be no reason why the tree should suffer - and still less reason for the hypothesis that their presence is beneficial to the plant.

Explanation of the persistence and modification of the stipules of Macaranga is less obvious. It would appear, however, that their peculiarities are connected with the food bodies which they sometimes bear. The fact that they are found on plants which have myrmecodomatia also complicates the problem. It is just as probable, however, that they have a physiological function connected with the food-bodies, as that they were developed solely for the purpose of attracting ants to the plant.

There are, of course, many other sides to the question. It may be argued that the "physiological function" subserved by the structures is in many cases hypothetical. It is, however, no more

hypothetical than the supposed benefit accruing to the plant from the presence of the ants. Again it may be pointed out that greater emphasis has always been laid on the sources of food than on the myrmecodomatia as adaptations for the attraction of ants. The complete absence of extra-floral nectaries and food-bodies from Tococa, Tachigalia and others of these myrmecophytes, and the fact that these plants were supposed to be myrmecophilous in spite of this fact, invalidates such an argument.

In short it appears reasonable to conclude from a consideration of these primitive myrmecodomatia, that their peculiarities of structure have been developed for normal physiological reasons, and that the ants appropriated the cavities so formed to shelter their eggs and larvae. They lived as parasites on the plants and, since the plants suffered no serious damage from their presence, the relationship has become more or less constant. It still obtains, however, only in those cases where the ants chance to find and to appropriate the preformed domatia.

HOLLOW RHIZOMES.

Hollow and swollen rhizomes provide the myrmecodomatia of Polypodium, Myrmecodia, Hydnophytum and other myremcophytes. The problem is substantially the same in every case; it has been most fully investigated for Myrmecodia. The results of these researches, as has already been indicated, is overwhelming evidence that the swellings and galleries are naturally formed, and probably

have a physiological function. Further, any slight advantage derived by the plant from the association with ants is too meagre to justify any explanation involving symbiosis. It appears, therefore, that the ants are parasites.

MYRMECODOMATIA in STEMS and BRANCHES.

These domatia may take several forms. The stems may be externally normal but hollow for practically their entire length, as is the case in Cecropia, Triplaris, Vitex, etc. In other cases the stems and branches present fistulose swellings either near the nodes (e.g. Plectronia, Cuviera, Cordia), in the middle of the internodes (e.g. Randia), or at the base of certain branches (e.g. Barteria). The stipular thorns of Acacia are comparable to these stem cavities both in respect of solidity and permanency. Their mode of formation is also somewhat similar. These myrmecodomatia represent the most highly developed form of myrmecophytes. They provide strong and lasting protection for the ants' nests, and often serve also as a source of food to the inhabitants through the callus-heteroplasias and the coccids.

There is every reason to believe, as has been pointed out in the descriptions of myrmecophytes, that the central cavities in stems, branches and thorns are formed naturally by the collapse of dried pith in the centres of these parts. It is probable that the ants accelerate the formation of the cavities by gnawing away the walls; this has been proved to be true in the case of Cecropia

by Fiebrig (1909). Schimper (1898) and others have admitted that the hollow stems are not adaptations to the ants; they are rather the result of economy of material in the strengthening of the stem, and are present before the ants colonize the plants.

The location and formation of the exit apertures of these myrmecodomatia present a more difficult problem. In a number of cases the apertures seem to be irregularly distributed; they appear to be excavated indiscriminately by the ants. In several myrmecophytes, however, the entrance holes are always excavated at definite spots. Thus in Vitex Staudtii they are regularly made at the nodes, one on each side, midway between the points of insertion of the leaves: in Cecropia they are made at the points marked by depressions or "prostomata" above the axils of the leaves: in Clerodendron fistulosum they are located just below the points of attachment of the leaves: in Cuviera and Plectronia they are found on opposite sides of the myrmecodomatia. In each of these cases, as has been pointed out, the particular location of the apertures is explained by various constant circumstances. In the case of Cecropia the depressions are formed by the pressure of the young axillary bud. In the other cases the points chosen for excavation by the ants are correlated with the phyllotaxy of the plant. In Vitex Staudtii and Clerodendron fistulosum the elements of the xylem are differentiated and distributed in such a way that the points chosen by the ants for entrance are particularly easy of excavation. In Cuviera and Plectronia the two sides of the

stem on which the entrance apertures are found are, as a result of the decussate phyllotaxy of the plants, markedly thinner than the adjacent sides.

The location of the entrance hole can, therefore, in all these cases be explained as being the result of the normal anatomy of the plant. The ants locate the thin spots and make their entrances at these favourable places. There would thus appear to be no necessity to explain the "prostomata" as adaptations to the ants.

How the ants are able to locate these "prostomata" is a question for the myrmecologist. Wheeler has suggested that ants may, through their extremely delicate tactile (or rather chordonotal) sense-organs, be able to select the thinnest point. He adds that their sense of smell may warn them against gnawing parts of the stem containing certain distasteful substances.

FEEDING HABITS of PLANT-ANTS.

Methods of Investigation.

Although the feeding habits of the ants which inhabit myrmecophytes is a very important aspect of the problem of myrmecophily, very little reliable information is available on the subject. The following methods of investigation have been used:

Field observation of the habits of the ants is naturally the primary source of information on the subject. No systematic work, however, has been done in this way. Thus it appears to have been

established that the Beltian and Müllerian food-bodies are collected by the ants, and that the extra-floral nectaries are frequently visited by them, but there are no critical and detailed field observations or experimental investigations as to the use to which they are put by the ants. Again it has often been assumed that if a nutrient tissue is gnawed by the ants it must be an important source of food. Fiebrig (1909), who himself made this mistake, records having seen Aztecae in young internodes of Cecropia, excavating the medulla and casting the fragments out of the domatia. Bailey (1922) insists that it must not be assumed that excavated medullary tissue is serving as a source of food: it may be removed solely for the purpose of cleaning or enlarging the domatia. The problem is complicated by the difficulty of observing ants in their natural habitat.

Examination of the faeces or contents of the alimentary tract of ants provides very little information because these insects take only fluid or semifluid foods into their stomachs. There is no recognisable form in these contents.

A certain amount of information can be derived from analysis of the contents of the infrabuccal sacs of the ants. Janet demonstrated that these sacs act as receptacles for detritus - which the imagines "remove by means of their toilet organs from their own bodies, from their progeny, and from their companions". They contain in addition food residues, whether removed from the body,

or solids separated from the fluid or semifluid substances that pass into the crop. The material thus accumulated is formed into a pellet which is finally cast out as a useless residuum or fed to a larva as in the case of the Pseudomyrminae. In the case of the Pseudomyrminae information can be obtained, in addition, from the trophothylaces of the larvae. H. von Ihering and Huber examined the infrabuccal pellets to get information about the origin of fungus-gardens during the founding of new colonies of Attine ants, but Bailey (1922 a.) appears to be the only observer who has examined them with reference to the feeding habits of plant-ants. He found that the pellets of Viticicola, the obligatory inhabitants of Vitex Staudtii contain no food from an outside source: the larval trophothylaces of Pachysimae from Barteria fistulosa contained substances obtained from both outside and inside the myrmecodomatia, including fragments of coccids: the pellets of Crematogasters from Cuvierae, Plectroniae, and Barteriae also contained substances both from within and without the myrmecodomatia but included no fragments of coccids. The difficulty of interpreting those results is greatly increased by the fact that there is present even in the larval trophothylaces some detritus which will not be consumed. The great variety of substances found in the pellets will be realised from the following quotation from Bailey (1922 a.) with reference to the pellets of Pachysima:

"Almost every pellet contains either a whole coccid larva, or one or more chunks of an adult coccid. In addition they

have a relatively large admixture of fragments of medullary tissue, containing the amber-coloured substance; aërial hyphae from the walls of the domatia; mites; nematodes; unicellular hairs of Barteria fistulosa; dirt; and numerous spores of many different types. In addition they contain bits of extraneous plant tissues, pollen, fragments of malaxated insects, etc."

From these sources of information a certain amount of information has been collected as to the feeding habits of the ants. This information will now be reviewed.

Medullary Tissue.

Reference has already been made to the danger of assuming that whenever medullary tissue is excavated by ants it is being used as food. It is equally impossible to draw the general conclusion that medullary tissue is never eaten by the ants. There can be no doubt that the ants scarify the walls of the myrmecodomatia of many or all of the myrmecophytes with hollow branches. They excavate the remains of the succulent pith and remove some of the thick-walled medullary tissue. Fragments of these tissues occur abundantly in the infrabuccal pellets of the imagines (Bailey 1922 a.), but no evidence is available as to whether these are food residues or detritus.

Amber-coloured substance.

Bailey (1922 a.) has used the term "amber-coloured substance"

to designate a coloured and hyaline material which occurs in the normal and abnormal tissues of certain myrmecophytes. He himself has demonstrated its presence in the layers of cells which jacket internally the myrmecodomatia of Cuviera, Barteria and certain of the Plectroniae. It is also found in the large thin-walled cells of the heteroplasias in these myrmecophytes. In a later paper (1923) he showed that it occurs in the tissues of the petiolar cavities of Tachigalia. The translucent amorphous material found in the cells of the peripheral layer of medullary tissue in the myrmecodomatia of certain Cecropiae is a similar or identical substance. Further investigation may reveal the fact that this amber-coloured substance occurs in many other myrmecophytes.

Bailey describes the substance as "a complex mixture containing proteins and carbohydrates". The material which he examined was viscous or solid; this may have been the result of preservation. If, on the other hand, it has not undergone solidification, Bailey supposes that the coccids must secrete substances which act upon it to render it sufficiently fluid to pass through their sucking mouth parts. That both the ants and coccids feed on the substance he does not doubt; it serves in addition as an excellent culture medium for fungi. The exact role, however, which it plays in the nutrition of ants, coccids and fungi requires to be more carefully investigated.

Fiebrig, it is interesting to note, observed this reddish-brown colour in 1900 and concluded that it is produced by oxidations

induced by formic acid. Such a hypothesis is, in the opinion of Bailey, not likely to be substantiated. Bailey's observations go a long way towards disproving it.

Fungi.

The great majority, if not all, of the ant-inhabited plants with woody domatia have a more or less luxuriant growth of fungi upon the inner walls of their cavities. Some writers have assumed that the fungi may serve as a source of food to the ants. There are very considerable differences, however, between the plant-ants and the truly fungivorous Attini which throw doubt on such a hypothesis. While the Attine ants are highly specialised and phytophagous, the others are cosmopolitan and more or less omnivorous. When it is considered, moreover, that the mats of hyphae may be purely adventitious (the spores being carried into the domatia either on the bodies of the ants or in their infrabuccal pouches), and that the hyphae may be cropped by the ants merely to prevent them from occluding or obstructing the galleries, it seems much more probable that the fungi are not eaten by the ants. This view is strongly supported by Miehe (1911) and Bailey (1922 a. and 1924). Though there can be no doubt that the ants do crop the fungi, there is no reliable evidence that they cultivate and feed upon these growths. In this case, as in that of the medullary tissue, it is more probable that the ants are merely house cleaning, and that the fungus is an unwelcome but inevitable intruder in the domatium.

Callus Heteroplasias.

The credit for having drawn attention to the importance of the heteroplasias as a source of food for the ants belongs again to Bailey (1922, 1923, etc.). The "stomatomes" or callus growths in the entrance apertures of Cecropia were described and figured, it is true, by Müller (1880) and H. von Ihering (1907), but neither of these writers realised their true significance as sources of food. It is probable that this function is not so important in Cecropia where the callus is formed only in the entrance holes.

In Cuviera, Plectronia, Barteria, and Vitex, there are found, as already described, within the myrmecodomatia excavations which contain peculiar callus-heteroplasias. Other extra-African myrmecophytes, upon further and more critical study, may be found to contain similar structures.* The question of the origin of these growths is important. Von Ihering suggested that the callus in the stomatomes of Cecropia is due to the stimulus of some substance excreted by the queens after they have entered the domatia. Bailey has proved that a purely mechanical stimulus is sufficient (1922 b.), and states (1922 a.) that "histological and other evidence indicates conclusively that the callus-heteroplasias.... are traumatisms induced by the ants".

* Such pits are not excavated in the Cordiae, probably because the myrmecodomatia of these plants are not jacketed internally by compact layers of thick walled cells. The coccids can therefore insert their setae into the soft nutritious tissues without the help of the ants. (Bailey 1924)

Bailey (1922 a.) also describes the probable origin of the pseudo-gall forming habit of the ants, with the intention probably of forestalling the suggestion that the lateral cavities and callus-heteroplasias of the myrmecophytes he has described may be adaptations for attracting ants. His interesting hypothesis may be summarised as follows:

> It is to be emphasised that the lateral cavities and nutritive callus-heteroplasias occur in plants of different growth forms (belonging to three distinct orders, Parietales, Tubiflorae and Rubiales) and are produced, not only by the "obligatory" Viticicola and Pachysimae, but also by the ubiquitous, "facultative" Crematogasters. The excavations are more regular both in size and position in Vitex Staudtii than in the flacourtiaceous and rubiaceous myrmecophytes.
>
> When mechanical injury disturbs the equilibrium of the tissues of a plant the general condition and physiological activity of these parts are changed. Cambial cells, when injured, tend to divide more actively, having been altered in polarity. This acceleration in growth generally extends to the overlying parenchyma and produces lateral outgrowths of delicate, thin walled, unlignified cells from the sides of the wound. These callus formations lead in time, if there is no interference, to a regeneration of the missing portions of the cambium, cortex, xylem and phloem. The callus-hetero-

plasias tend to contain a considerable concentration of food-substances (protein, fat, sugars etc.).

The entrance and exit apertures of myrmecodomatia are frequently occluded by such wound-tissues unless kept open by the ants. In cleaning the holes the ants are forced to gnaw upon the callus-heteroplasias: they discover its nutritive value and in many cases endeavour to increase its volume by the most direct means - by cutting through to the cambium. The callus-heteroplasias grow better inside than outside the domatia. When the normal tissues jacketing the domatia contain the nutritive amber-coloured material, this substance is found also in the callus, increasing its value to the ants.

In view of these facts, it is not surprising that the pseudo-gall-forming habit should have originated among several genera of African twig-inhabiting ants.

The problem of determining the exact nutritional significance of the callus-heteroplasias is complicated by the presence of the coccids which feed upon these tissues. The case of Vitex Staudtii seems to be exceptional. In this myrmecophyte the excavations in which the heteroplasias grow are more regular and deeper than in the other ant plants such as Cuviera, Plectronia and Barteria. No coccids are found in the myrmecodomatia of Vitex Staudtii and it is evident that the Viticicolas themselves feed on the heteroplasias. The evidence for this belief has already been de-

tailed in section II.

In the other myrmecophytes the question arises whether the heteroplasias are induced by the ants for their own consumption or solely for feeding the coccids. Further observation is required before this question can be answered. Bailey (1922 a.) sums up the present position thus:

> "Histological evidence indicates that the nutritive layer is gnawed and rasped by the ants, and fragments of this tissue occur in the pellets of Crematogasters, but these facts in themselves do not afford a solution of the difficulty. Nor does the absence of the coccids in certain of the myrmecodomatia which contain callus-heteroplasias prove that the chief function of these traumatic tissues is not the provision of food reservoirs for Coccidae."

Coccids.

Belt (1874) stated that in Cecropia the Aztecae "do not obtain their food directly from the tree, but keep brown scale-insects (Coccidae) in the cells (i.e. domatia), which suck the juices from the tree, and secrete a honey-like fluid that exudes from a pore on the back, and is lapped up by the ants." Fiebrig (1909) alone has disagreed with this opinion: the coccids in Cecropia, he says, "in keinem direkten Verhältnis zu diesen Ameisen stehen". Bailey, however, has actually observed the ants soliciting and consuming the sugary excretions of the coccids. In those

myrmecophytes in which lateral cavities and callus-heteroplasias are formed the coccids invariably lie in the depressions and suck their nourishment from the nutritive tissue of the callus. It has been established (vide supra) that the ants and not the coccids make the pits. In Vitex Staudtii alone of these ant-plants coccids are not generally present.

There is some doubt as to how the coccids come to enter the domatia. Üle (1906) and others assume that they are taken in by the ants. Bequaert (1922), however, has observed coccids entering the domatia of Barteria and Cuviera of their own accord. It seems unlikely that the colonies of coccids should be purely adventitious in every case.

In addition to being tended as "milch cows" by the ants, the coccids themselves are often eaten and fed to the larvae. This occurs at least in those cases where the ants are Pseudomyrminae or Pachysimas (Bailey 1922 a., and 1923). Though the coccids are thus reduced in number they are never completely exterminated in any one domatium.

Nematodes.

Nematodes frequently live in the detritus of the ant colonies, i.e. accumulations of voided pellets, liquid faeces, fragments of malaxated insects, triturated plant tissues etc. Certain of the nemas are highly specialised morphologically, and are adapted to feeding upon the delicate hyphae of fungi which flour-

ish in the refuse of the ants. In the case of the Pachysima and Pseudomyrma ants the nematodes are found in the infrabuccal pellets and fed to the larvae. Whether they occur in the pellets as detritus or food-residues is unknown (Bailey 1922 a. and 1924).

Extrafloral Nectaries.

Extrafloral nectaries have been defined as glands, secreting saccharine substances, located on the vegetative organs of plants. They are found on several myrmecophytes but occur also on numerous plants which provide no domatia for the ants. On both types of plant they are very often visited by ants which eagerly collect the sugary secretion.

There has been considerable discussion in the past as to the true significance of floral nectaries; whether their function is physiological or ecological. Though it is still by no means certain that they are not useful to the plant in a physiological way, it has now been definitely established that they attract pollinating insects which in turn assure or greatly facilitate cross-fertilization. There has been a natural tendency to look for an analogous relation between ants and extra-floral nectaries. Thus Delpino asserted in 1874 that the chief function of these glands 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 larvae. He added that they performed a subordinate function by detaining ants and thus keeping them from

the floral glands where they would only prevent pollination by frightening insects away. This latter service was judged by Kerner von Marilaun to be the main purpose of the nectaries. Most of the supporters of the theory of myrmacophily accepted Delpino's hypothesis. Schimper, however, is commonly misrepresented as having fully endorsed this theory. His true opinion is indicated by the following quotation:

> "The most probable view at present seems to be that extrafloral nectaries fulfil a still unknown function, which is independent of the ants, but is in some way connected with a warm climate, and that they have only secondarily become myrmecophilous organs." (Schimper, 1898)

The evidence in favour of a hypothesis such as Delpino's may be summarised as follows:

(1) Innumerable cases have been observed where ants frequented the glands.

(2) Extrafloral nectaries are more common in the tropics where ants are more common.

(3) The plants need protection against phytophagous insects and caterpillars. It is contended that the ants constitute the required bodyguard.

(4) The nectaries are often found to be well developed on the parts of the plant which most need protection, viz: the young leaves. (This has frequently been denied - vide infra).

When the theory of myrmecophily began to be seriously opposed, Delpino's theory of extrafloral nectaries was called in question. Madame M. Nieuwenhuis von Üxküll-Güldenbrandt (1907) made a very thorough investigation of the subject and was led to

deny the earlier assumptions. She was forced to admit that the true function of the nectaries was unknown, but she concluded that "die Pflanzen mit extrafloralen Zuckerausscheidungen durch einen Ameisenbesuch nicht nur keinen Vorteil geniessen, sondern haufig sogar grossen Schaden erleidern." In this opinion she has been supported by almost all the later writers. The arguments in favour of this view may be summarised thus:

(1) Observation shows that the extrafloral nectaries, while present in a great number of species, are in many of them seldom if ever visited by ants. This fact was admitted even by Schimper.

(2) The glands attract not only ants but also many other insects which are harmful to the plant, and are in no way deterred by the presence of the ants.

(3) It has not been established that the ants protect the plant in any way. It is more probable that they are harmful.

(4) The supposition that ants may be limited in their feeding propensities in such a way that the extrafloral nectaries will prevent their visiting the floral nectaries cannot be admitted. Ants are, in fact, often found on the flowers of plants bearing nectaries on the vegetative organs.

(5) Blatter (1928) asserts that nectaries are very often absent from the young parts of the plant where they would be most needed, while they develop freely on older organs.

The evidence is too conflicting to allow of any final con-

clusion, but it may safely be said that the probabilities are against the hypothesis that the extrafloral nectaries are adaptations for attracting ants.

Food-bodies.

In support of the theory of myrmecophily great weight has been ascribed to the occurrence on certain myrmecophytes of so-called "food-bodies". These are white, oval, or pear-shaped bodies composed of cells rich in proteids and fatty oils, so that they cannot be regarded as excreta (v. Fig. 3). They are found on Acacia (Beltian bodies), on Cecropia (Müllerian bodies) and on Macaranga. Their position and particular nature on each of those myrmecophytes have already been described. Similar bodies occur also on many non-myrmecophytic plants (e.g. Leea hirsuta Blume, and Pterospernum javanicum (Junghuhn), where they are eagerly collected by ants.

Schimper (1888) regarded these corpuscles as metamorphosed glands which have become highly specialised allurements for attracting ants. Rettig (1904) and others pointed out that these bodies were found on non-myrmecophytic plants, and Üle (1906) expressed the opinion that the expenditure of carbohydrates and nitrogenous substances contained in these corpuscles is not compensated for by the protection which the ants afford to the plants. With the growing doubt that the ants are of any benefit to the plants Schimper's original hypothesis that the food-bodies are

adaptations to ants has met with less support. No other satisfactory explanation, however, has as yet been suggested.

Though it has been established beyond doubt that the food bodies are collected by the ants, careful field observations are required to determine the exact nutritional significance of these structures.

ADVANTAGES TO THE PLANTS.

The crux of the whole problem of myrmecophily lies in the question of the possible advantage or advantages accruing to the plants from the presence of the ants. If there is a symbiotic relation the plants must derive some advantage: if there is no advantage to the plant there can be no myrmecophily. That the ants benefit is, of course, beyond doubt: they obtain lodging, and in most cases also food, from the host plant.

Various possible benefits to the plant have been suggested by various writers. Ridley (1910) has expressed the opinion that Dischidia rafflesiana may benefit from the fact that the ants supply food in the form of nest débris to the rootlets enclosed in the pitchers. Similar suggestions have been made by several writers with reference to Myrmecodia and other myrmecophytes with hollow rhizomes: the plants may derive nourishment from the detritus deposited by the ants in the domatia. Both these hypotheses, however, have reference only to particular cases and are of little significance in a general theory of myrme-

cophily. The same may be said of the suggestion put forward by Forbes (1885) that the ants inhabiting Myrmecodia serve the plant by removing injurious secretions from the papillae in the walls of the myrmecodomatia. It has also been demonstrated that the papillae are not excretory organs (vide supra). Bequaert (1922) has pointed out that an inhabited individual of Barteria fistulosa may be surrounded by an open patch where the ants have cleared away the heavy undergrowth probably by nipping all shoots; he suggests that the plant may benefit from the removal of competition. Such an occurrence, however, is too rare to allow of any general conclusions.

The only suggestion, in fact, which has ever been of any importance is the contention of Belt, Beccari, Schimper, Schumann, etc., that the ants defend the plants against phytophagous enemies. The evidence for and against this hypothesis has been detailed in the section dealing with myrmecophytes. Since the verdict on this question is so vital, a review will be given here of the various arguments which support or oppose the hypothesis that the ants defend the plant against its enemies.

Protection of Plants.

Belt (1874) in propounding his theory of myrmecophily asserted that the ants inhabiting Acacias "form a most efficient standing army for the plant, which prevents not only the mammalia from browsing on the leaves, but delivers it from the attacks of

a much more dangerous enemy - the leaf-cutting ants". He grew some Acacia plants from seed: they were not inhabited by ants. Of these he writes: "The leaf-cutting ants attacked the young plants, and defoliated them, but I have never seen any of the trees out on the savannahs that are guarded by the Pseudomyrma touched by them, and have no doubt the acacia is protected from them by its little warriors." In the same way he appeared to "have no doubt" that Cecropiae and Melastomae inhabited by ants are similarly protected.

The unfortunate thing is that so little doubt should have been thrown on this hypothesis in the first thirty years after it was first made by Belt. All the other writers considered that it was required of them only to reassert the fact that myrmecophytes were protected by their guest ants. If they had realised how fundamental the problem was, and how open to question the explanation advanced, they might have put their evidence in a statistical form which would have been of some use to later investigators. The following quotations are typical. Schimper (1898) states that

> "The leaf-cutting ants show such a preference for the foliage of Cecropia, that, at Blumenau, Fritz Müller and I found every one of the uninhabited trees, which are rare, had its leaves bitten down to the midrib, whereas not a single tree with a protective army of ants showed a trace of such injury."

Schumann (1888) assumed that myrmecophytic Melastomae are protected by their ants, because they are "in dem Herbarien niemals angefressen oder irgendwie durch die Einwirkung unberufener Gäste verletzt."

In the last 30 years many investigators have contended that Belt, Müller, Schumann, Schimper, etc., exaggerated the destructiveness of the leaf-cutting ants and the protection afforded by the guest-ants. Üle (1906) writes:

"Zahlreiche Beispiele gibt es nun, wo die Myrmecophyten trotz des Ameisenschutzes von vielen Tieren geschadigt oder zerstört werden."

Rettig (1904), von Ihering (1907), Fiebrig (1909), Wheeler ~~(1913)~~, and many others, agreed that the guest ants do not protect the great majority of myrmecophytes against Attine ants and other enemies. Fiebrig expresses the opinion that the constant loss suffered by a Cecropia tree from the depredations of Azteca itself involves a more serious drain upon its vitality than the occasional raids of the leaf cutters, and that the presence of the guest-ants even encourages the assaults of such formidable foes as woodpeckers and internally feeding lepidopterous larvae. H. von Ihering considers that the plants require and obtain no protection other than their own vegetative power:

"Die teilwise oder ganz entblätterten Gewächse sterben nicht ab, sondern treiben sehr rasch neue Blätter und erhol-

len sich schnell, auch wenn die Ameisen von Zeit zu Zeit die Prozedur des Blattschneidens wiederholen."

Bailey (1922) after a careful investigation of Cecropia concluded that -

"Attine ants show no preference for the foliage of Cecropia, and rarely attack either inhabited or uninhabited trees. Although Aztecas tend to prevent other ants from visiting the terminal portions of the adult Cecropias, they do not protect the juvenile individuals."

Wheeler and Bequaert (1929) write with reference to Duroia saccifera:

"It is interesting to note that, in spite of the pouches being inhabited by ants, the young leaves of this plant were badly damaged by leaf-cutting ants (Attini), while the older leaves were eaten by caterpillars."

Such quotations could be multiplied indefinitely. Many others have already been given in the section dealing with particular myrmecophytes. It is clear, however, that they are of no more weight as evidence than the statements of Belt, Schimper and Schumann. What is required is not records of particular cases or vague and general statements but statistical evidence from detailed investigations. It would appear that such an enquiry has been made in only one case. Melin (1930) made careful records of the correlation between inhabitation and damage suffered, for a large

number of Tococa plants. His results, (vide supra p.66) led him to the conclusion that the guest-ants provided little or no protection to the Tococa plants.

It is evident that, until many more systematic investigations have been made, no definite and final conclusion can be drawn as to the degree of protection afforded to myrmecophytes by the ants they shelter. Meanwhile, however, it would seem probable from the available information that, though the protection provided is not always negligible, yet it is never sufficient to justify the conclusion that the relation between ant and plant is one of symbiosis; it is never so considerable as to repay the plant for all it loses in providing food and shelter for the ants.

THEORIES of MYRMECOPHILY.

Before finally summing up the present status of the problem of myrmecophytism, it will be advantageous to summarize the various theories that have been propounded. In the following pages there will be some repetition of facts which have already been mentioned in the historical summary of Section I and elsewhere. This is unavoidable if the history of the problem of myrmecophily is to be adequately reviewed. Little mention will be made of the work of writers who did not formulate original theories. In most cases reference has been made in preceding sections to their investigations.

Belt's Theory of Symbiosis.

Belt observed various species of Acacia, Cecropia and

Melastomae and formulated an ingenious theory of myrmecophily. His conclusions, published in 1874, are of interest not only because they initiated the controversy which has been waged for sixty years on the subject of myrmecophily, but also because they embody all the fundamentals of the only hypothesis which has obtained any considerable degree of support during that period. Other writers have suggested slight additions and modifications but these have seldom been generally accepted, and, even when accepted, have been of little importance. Delpino, working independently, suggested a similar explanation of extra-nuptial nectaries about the same time, but he did not actually formulate his theory of myrmecophily till many years later.

Belt is often misrepresented by writers who quote his remarks concerning Acacia trees as expressing his whole opinion on the problem of ants and plants. In actual fact his conclusions are slightly different for Acacia, Cecropia and Melastomae, as is shown by the following quotations:

Having pointed out how the ants obtain food and shelter from the Acacias and give protection in return, he writes:

"I think these facts show that the ants are really kept by the acacia as a standing army, to protect its leaves from the attacks of herbivorous mammals and insects."

With reference to Cecropia he concludes:

"This case is not like the last one (i.e. Acacia), where

the tree has provided food and shelter for the ants, but rather one where the ant has taken possession of the tree, and brought with it the Coccidae; but I believe that its presence must be beneficial."

Since he makes no mention of the food-bodies on Cecropia it may be supposed that he failed to observe these; otherwise he might not have drawn any distinction between that genus and the Acacias.

He notes the presence of coccids in the leaf pouches of the Melastomae and supposes that in this case

"we have an instance of two insects and a plant living together, and all benefiting by the companionship. The leaves of the plant are guarded by the ants, the ants are provided with houses by the plant, and food by the Coccidae or Aphides, and the latter are effectually protected by the ants in their common habitation."

Though Belt's theory implies "natural selection", he himself made no reference to it as the cause of development of the structural peculiarities exhibited by ant-plants.

Delpino's Hypothesis.

A promise, at least, of a theory of myrmecophily is contained in Delpino's paper published in 1874:

"I do not hesitate to announce now that the chief function of these (extrafloral) 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 larvae."

It was not till 1889, however, that he expressed the full hypothesis:

"In the case of myrmecophilous species, the plant works for the ant in two ways, either in supplying a sugared food, or in furnishing suitable lodgings; and the ant works for the plant in defending it against its enemies." (Trans: Bailey, 1922 a.)

Beccari's Hypothesis.

Beccari strongly supported the theory that the ants and the plants live in a symbiotic relationship. He endeavoured to account for the origin of the structural modifications of various myrmecophytes upon the basis of the Inheritance of Acquired Characters. His view is well summarized in a passage quoted by Ridley (1910).

"The nature, origin and function of the ant-harbouring organs, not only of Korthalsia, but in numerous myrmecophilous plants, and most of all in Myrmecodia and Hydnophytum, have been much discussed: with regard to this subject I retain my old opinion that such organs are now hereditary, but that they owed their origin to the effects of the stimulus exerted by ants on certain organs of the plants, of which tissues were

capable of a reactive power during the remote period of the plasmation epoch, when heredity had not yet acquired its actual conservative power."

Müller, Schimper, Schumann.

The work of Müller (1880), Schimper (1888) and Schumann (1888 and 1891) is outstanding in support of the theory of myrmecophily. This hypothesis is often referred to as "Schimper's Theory"; the only justification for this usage lies in the fact that Schimper emphasised the importance of Natural Selection as explaining the origin of the structural peculiarities. All, however, adduced considerable evidence, particularly with reference to Cecropia, to show that myrmecophytism is a true symbiosis. They sought to prove that the food-bodies, extrafloral nectaries and many of the peculiar structural modifications of myrmecophytes are adaptations for the purpose of atttracting ants, and that the ants actually protect the host plants.

Though Schimper admitted that the hollow stems of myrmecophytes are natural productions, he believed that the prostomata as well as the food-bodies and nectaries were adaptations to ants. The following remarks with reference to the groove above the axillary bud in Cecropia are significant in this connection:

"At the phylo-genetic commencement of symbiosis, the ants bored an entrance through the groove, evidently because the wall was somewhat thinner there, and in particular, in accord-

ance with a custom that is almost always followed and is connected with the domestic arrangements, they bored as much as possible in the upper part of their dwelling. All features that facilitate boring through this place must have been retained in the struggle for existence, and been further added to through selection. They finally led to the differentiation of the thin weak diaphragm that has been described." (Schimper 1898)

Buscaloni and Huber.

In 1900 Buscaloni and Huber published a short paper entitled "Eine neue Theorie der Ameisenpflanzen". Observing that myrmecophytous plants are usually found on ground which is periodically inundated, they concluded that the ants resort to the plants, or originally resorted to the plants, to escape the floods. They add also the following statement:

"Das den betreffenden Pflanzen jedoch durch die Ameisen auch ein Schutz erwuchs gegen allerlei Schadlinge und dass infolgedessen eine allmähliche Auswahl der myrmekophilen Merkmale bewirkt wurde, ist sehr wahrscheinlich."

This view had been proposed by Spruce in 1869 but his paper was not published till after 1900.

Spruce and Wallace.

In 1869 Spruce read to the Linnaean Society a paper in which

he tried to account for the structural peculiarities of myrmecophytes on the basis of Inheritance of Acquired Characters. The Council of the Society refused to authorize the publication of certain opinions which Spruce considered fundamental, with the result that the paper was not made public till 1908. It was then edited by Wallace. Though the paper was written before Belt had published his conclusions it is recorded here because, in the history of the problem of myrmecophily, its chronological position corresponds to the date of its publication.

Spruce expresses his belief in the Inheritance of Acquired Characters in the following passage:

> "I have reason to believe that all of these apparently abnormal structures have been originated by ants, and are still sustained by them; so that if their agency were withdrawn, the sacs would immediately tend to disappear from the leaves, the dilated branches to become cylindrical, and the lengthened branches to contract; and although the inheritance of structures no longer needed might in many cases be maintained for thousands of years without sensible declension, I suppose that in some it would rapidly subside and the leaf or branch revert to its original form."

He supposed that the ants induced the formation of the abnormalities to provide themselves with domatia during periods of inundation, for he asserted that the majority of myrmecophytes

occur in low lying land which is either swampy or periodically inundated. He supported his hypothesis by the observation that those trees which are entirely submerged during periods of high water are never inhabited by ants. The ants resort only to species which are only partly covered. Buscaloni and Huber, as has been pointed out, developed a theory on the same premises.

It is interesting to note that Spruce did not consider that the relationship between plant and ant is symbiotic. This is indicated by the following statement in a letter to Darwin:

> "The ants cannot be said to be useful to the plants, any more than fleas and lice are to animals; and the plants have to accommodate to their parasites as best they may."

Wallace, however, edited Spruce's paper in the light of all the work done on myrmecophily at the end of the nineteenth century. He supported the theory of myrmecophily and emphasised the effect of Natural Section.

> "Spruce's error was in not recognising that the ever present variability in all the parts and organs of plants furnished the MATERIAL, and the survival of the fittest the AGENCY, by which these, as well as all other specific modifications of plants, have been brought about; and that this is a far more powerful, as well as a more exact and certain, mode of doing so than the hereditary transmission of mutilations, the effect of which would in many cases be the reverse of beneficial."

The evidence seems to show that the ants are useful to the plants - "in which case their becoming hereditary is merely a question of variability in the plant, and the continued preservation of those whose variations were in the direction of utility to the ants."

These phenomena lead "to the establishment of the general principle, that no special adaptation of one organism to another can become fixed and hereditary unless it is of direct utility to both."

Chodat and Carisso.

In 1920 Chodat and Carisso published, "Une nouvelle théorie de la myrmécophilie". They assert that the hypertrophied portions which form the domatia of myrmecophytes are in reality galls which become inhabited by ants after they are abandoned by gall forming insects. They drew this conclusion from the fact that they found eggs and larvae of hymenopterous parasites in immature myrmecodomatia of species of Cordia and Acacia. They added, with no apparent justification.

"Il y a tout lieu de penser que les formicaires des autres plantes myrmécophiles, quand ils se présentent comme des renflements, ont une origine analogue."

This theory was strongly opposed by De Wildeman (1921), and was finally disproved by evidence adduced by Bequaert (1922) and Bailey (1923 and 1924).

The Theory of Myrmecophily.

There are three main theories of myrmecophily:

(1) Belt's Theory of Symbiosis.

(2) Buscaloni and Huber's Theory.

(3) Chodat and Carisso's Theory.

Buscaloni and Huber's theory has received no support except from Spruce, who, it must be remembered, wrote in 1869. It is an impossible contention that all myrmecophytes grow in ground which is periodically inundated. Only the Ant-acacias of the savannahs of South America need be cited to disprove the hypothesis.

The theory proposed by Chodat and Carisso has also received no support and has, as indicated, been adequately disproved.

There is thus left only the hypothesis that the ants and plants live in symbiotic relationship. This may be called T H E Theory of Myrmecophily. There are, however, two varieties of this theory. First there is the hypothesis of Schimper, which regards the modifications of the plants as being the result of natural selection, working through the variability of the plants and the tendency of the fittest to survive the less fit. Secondly, there is the Spruce-Beccari hypothesis which explains the structural peculiarities as being inherited and acquired characters. It is to be noted that while Spruce regarded the modifications as mutilations, Beccari believed them to be beneficial to

the plant. The general taboo on the Inheritance of Acquired Characters has so discredited their hypothesis that it has received very little support, or even serious consideration, until quite recently by writers who opposed the theory of myrmecophily. We may, therefore, define the Theory of Myrmecophily as a hypothesis to the effect that the peculiar structural modifications of myrmecophytes have developed as a result of natural selection, as adaptations for the attraction of ants, which are beneficial to the plant because they protect it against phytophagous enemies.

CRITICS of MYRMECOPHILY.

Üle (1901, 1906 and 1907), Rettig (1904), H. von Ihering (1907), Madame Nieuwenhuis von Üxküll-Gülderbrandt (1907), Fiebrig (1909), Wheeler ~~(1913)~~, Bequaert (1922), Bailey (1922 etc.) Möbius (1925), and many others have opposed the theory of myrmecophily. They have based their objections on two main arguments:
(1) that the ants are not sufficiently effective guardians of the plants to justify a theory of symbiosis accounting for the origin of the various structural modifications of myrmecophytes through the action of Natural Selection.
(2) that many plants which are neither inhabited nor frequently visited by ants are provided with pseudodomatia, prostomata, food-bodies, extrafloral nectaries, etc.

They infer that the ants are parasites taking full advan-

tage of the structural peculiarities and sources of food supply of the plants. The following conclusions are more or less typical.

Üle (1906) writes:

"Die Ameisen haben diejenigen Pflanzen, welche ihnen dienlich waren, mit vielen Geschick oder Sharfsinn angewählt und je nach ihren Bedürfnissen benutzt, und auf die bewohnten Gewächse höchstens einen Einfluss ausgeübt, etwa wie wir bei den mehr wild wachsenden Nutzpflanzen."

Rettig (1904) expresses his conclusion in the following interesting way:

"Meiner unmassgeblichen Meinung nach gibt es wohl Pflanzenameisen in Hülle and Fülle, aber (wenigstens im strengsten Sinne des Wortes) wenig oder überhaupt keine Ameisenpflanzen",

and H. von Ihering thus:

Wenn ich oben äusserte dass die Cecropia adenopus ebenso gut ohne Aztecas bestehen könne wie der Hund ohne Flöhe, so führt uns das direkt zu der Überzeugung, dass das Verhältnis der Aztecas zu ihrer Wirtspflanze eher einen Fall von Parasitismus darstellt, als einen solchen von echter Symbiose."

De Wildeman (1921) regards myrmecophytism as "parasitisme en général très néfaste au myrmécophyte," and Bailey (1922 a.) sums up the problem of myrmecophytism as follows:

"Certain plants tend - for reasons which are at present obscure - to form extrafloral nectaries, food-bodies, prostomata, saccate leaves, fistulose branches, and other pseudodomatia, etc. In many cases, but by no means in all, these structural modifications of plants are taken advantage of by ants in their search for food and domatia. The myrmecophytic relationship which results is purely a case of parasitism in which all of the advantage lies with the ants."

That the critics of the theory of myrmecophily have established the two main arguments (vide supra) on which they base their conclusion cannot be denied. The weakness of their case lies rather in the fact that they have failed to provide a convincing hypothesis to account for the origin and functional significance of the various inherited structural peculiarities of myrmecophytes. The majority of them have been content to admit that the true function of the nectaries and food bodies is unknown. Schimper's explanation of the hollow stems of Cecropiae as due to mechanical causes is generally assumed to apply to all similar domatia but no explanation has been forthcoming of domatia of other types - e.g. the leaf-pouches of Tococa. It is true that the work of Treub (1883 and 1888), Rettig (1904), Miehe (1911) and others indicates that the galleries and papillae of Myrmecodia have a physiological function, but their results are neither conclusive nor generally applicable.

Probably the most promising line of approach is to explain the structural peculiarities as adaptations to the ants though these be useless, or even injurious, parasites. It has generally been assumed, apparently unreasonably, that modifications will not appear in a plant unless they are directly or indirectly useful. Is it not possible that the presence of the ants has stimulated the formation of structures whose purpose is rather to appease the ants than to attract them? Such a view was implied by Üle (1906 etc.) in such remarks as that quoted above. Shelford (1916) expressed it more clearly, as is shown by the following quotation:

> "If one plant can inherit the power to produce a definite pathological structure, I do not see why another cannot inherit the power to produce a structure adapted to harbour with least damage to itself guests that certainly will not fail to make their appearance."

This theory was most explicitly stated by Möbius (1925). Becher in 1917 applied the term "fremddienliche Zweckmässigkeit" to the production of plant galls, which, he concluded, are of advantage only to the parasite, and are hurtful to the host plant. "Fremddienliche Zweckmässigkeit" might be translated as "a relationship in which one organism is serviceable to another foreign ~~body~~ organism out of expediency" or more colloquially "making the best of a bad job". Möbius (1925) applied this principle to

myrmecophytism. He refuses to admit that if the structural peculiarities of the ant-plants were made for the benefit of the ants, the plants must also derive benefit from them and also from the ants themselves.

"Es noch andere Fälle gibt, in denen ein Parasit bei seinen Wirt morphologische und physiologische Veränderungen hervor-ruft, die nicht nur rein zu Nutzen des Parasiten sondern sogar zum Schaden des Wirtes sich ausbilden."

And again:

"In den Gallen haben wir Gebilde, die ganz entschieden eine fremddienliche Zweckmässigkeit aufweisen. Wir können nun auch die Eigenschaften, durch welche die sogenannten Ameisenpflanzen charakterisiert sind, als Äusserungen einer fremddienlich Zweckmässigkeit betrachten."

In other words, the plant, being occupied by a horde of ants, makes the best of a bad job by the development of adaptations which will appease the hungry ants and keep them from doing any real damage to the plant. The structural peculiarities are protective devices against the too pressing attention of ants, rather than devices to attract these insects. It is interesting to note that Spruce's (1908) hypothesis differs very little from that expressed by Möbius.

Melin (1930) approached the problem of myrmecophily from a new angle. He wished to find out whether myrmecophytism could

provide any ecological evidence for the theory of selection. He defines hereditary adaptation as "a special structure or a special condition developed orthogenetically in relation to environment", and concludes that:

> "We cannot explain the domatia in these plants inhabited by ants (and of course not extrafloral nectaries and food-bodies either) as an adaptation to ants that has originated through selection."

Melin reached this conclusion on the basis of the detailed statistical investigation of Tococa trees to which reference has already been made.

All the critics of myrmecophily are agreed that the relationship between ants and plants is not symbiotic, but that the ants are parasites on the plants. They disagree, however, as has been shown, as to the cause of origin of the structural modifications of myrmecophytes. This disagreement appears to be based on the difference between Darwinism and Neo-Lamarckism. Darwinists assume that an adaptation must be "useful", "purposeful" or what is called "favourable to life". The peculiarities of myrmecophytes, therefore, from the point of view of Darwinism, cannot be adaptations to ants unless the relationship between ants and plants is symbiotic. From the standpoint of Neo-Lamarckism, on the other hand, selection merely plays an inferior part and the process of evolution is not affected by the "utility" of structural modifica-

tions. To Neo-Lamarckists, therefore, the peculiarities may be adaptations to ants although the ants be parasites.

CONCLUSION.

Any theory of myrmecophytism must still be a matter of personal opinion, for although the available evidence has been considerably increased by the recent work of Bequaert, Bailey, Melin and others, it is not yet possible to draw any definite and final conclusions. The following statement, therefore, expresses only the present status of the problem of myrmecophytism.

Certain plants show structural peculiarities such as fistulose stems, hollow nodal or internodal hypertrophies, hollow petioles, saccate leaves, enlarged stipular organs, etc., and sometimes in addition extrafloral nectaries or food-bodies. The origin and function of these structures is still obscure. In a great many cases these hollow stems etc. are utilized by ants as domatia, and the nectaries and food-bodies used as sources of food. The ants usually have to construct entrances to their new homes. Some of these ants are obligatory and others facultative inhabitants of the myrmecophytic plants. In many cases the domatia contain, in addition to the ants, growths of fungi and numerous nematodes and coccids. The coccids usually feed upon certain traumatic tissues induced by the ants; the ants solicit and feed upon the exudates of the coccids, and in some cases feed

also upon the coccids themselves, the nematodes and the traumatic tissues. They obtain carbohydrate from the extrafloral nectaries, and fat and protein from the food-bodies when these are present. The ants thus obtain both food and shelter from the plants. It appears to be unusual, however, for the ants to have no extraneous sources of food.

The ants, in a few cases, provide to the plant a certain amount of protection against phytophagous enemies, but in no case is this protection such as could be supposed to compensate for the loss suffered by the plant, or to justify a hypothesis of a symbiotic relationship. The ants appear, therefore, to be parasites upon the plants, availing themselves of the structural peculiarities in a singularly efficient manner.

BIBLIOGRAPHY.

A very exhaustive Bibliography of the Relations between Plants and Ants has been compiled by Bequaert (1922). The following list is of books consulted in the preparation of this essay. Mention should be made also of one book excluded for reasons of language difficulties, viz., Beccari's famous work upon the myrmecophytes of Malesia: "Plante ospitatrici ossia piante formicarie della Malesia e della Papuasia". Malesia 11, 1884-1886. 340 pp. 65 Pls. Delpino's work is not represented for the same reason.

Anonymous. 1888. "Ants and Plants". Gardeners' Chronicle, (3) 111. p. 279.

Bailey, I.W. 1922a. "The anatomy of Certain Plants from the Belgian Congo, with Special Reference to Myrmecophytism". Bull. Amer. Mus. Nat. Hist. XLV, pp. 585-622.

1922b. "Notes on Neotropical Ant-Plants". 1. Cecropia Angulata sp. nov." Bot. Gaz. LXX1V. pp. 369-391.

1923. "Notes on Neotropical Ant-Plants. 11 Tachigalia Paniculata Aubl". Bot. Gaz. LXXV. pp. 27-41.

1924. "Notes on Neotropical Ant-Plants. 111 Cordia Nodosa Lam." Bot. Gaz. LXXV11. pp. 32-49.

Beccari, O. 1904. "Wanderings in the Great Forests of Borneo". London. XX1V + 424 pp.

Becher, E. 1917. "Die fremddienliche Zwechmassigkeit der Pflanzengallen und die Hypothese eines uberindividuellen Seelischen". Leipzig, 149 pp.

Belt, Th. 1874. "The Naturalist in Nicaragua". London. XV1 + 403 pp.

Bequaert, J. 1922. "Ants in their Diverse Relations to the Plant World". Bull. Amer. Mus. Nat. Hist. XLV. pp. 333-584.

Blatter, E. 1928. "Myrmecosymbiosis in the Indo-Malayan Flora". Journ. Indian Bot. Soc. V11. pp. 176-185.

Buscaloni, L. and Huber, J. 1900. "Eine nene Theorie der Ameisenpplanzen". Beih. z. Bot. Centralbl. 1X. 2 pp. 85-88.

Chodat, R. and Carisso, L. 1920. "Une nouvelle théorie de la myrmécophilie". C.R. Séances Soc. Phys. Hist. Nat. Geneve, XXXV11. No. 1. pp. 9-12.

De Wildeman, E. 1921. "Sur les théories de la myrmecophilie". C.R. Ac. Sci. Paris. CLXX11. pp. 124-126.

Doctors Van Leeuwen, W. 1921. "Kurze Mitteilung uber Ameisen-Epiphyten aus Java". Ber. Dtsch. Bot. Ges. XLV11. pp. 90-99.

F. A. D. 1909. "Is the association of ants with trees a true symbiosis". Nature. LXXX1. No. 2070. p. 23.

Fiebrig, K. 1909. "Cecropia Peltata und ihr Verhaltnis zu Azteca Alfari, zu Atta sexdens und anderen Insekten, mit einer Notiz über Ameisendornen bei Acacia cavenia". Biol. Centralbl. XX1X. pp. 1-16, 33-55, 56-77.

Forbes, H. O. 1880. "Notes from Java". Nature, XX11. p. 148.

1885. "A naturalist's wanderings in the Eastern Archipelago". London. X1X + 536 pp.

Goodchild, J. G. 1903. "Ants in Relation to Flowers". Trans. Edinburgh Field Soc. V. pp. 10-23.

Ihering, H. v. 1907. "Die Cecropien und ihre Schutzameisen". Engler's Bot. Jahrb. XXX1X. pp. 666-714.

Jack, W. 1825. "Account of Lansium and some other genera of Malayan plants". Trans. Linn. Soc. London, X1V. pt. 1, pp. 114-130.

Kerner von Marilaun, A. 1894-1895. "The natural history of plants : their forms, growth, reproduction and distribution". Trans. by F.W. Oliver, London. Vol. 1, 1894, 777 pp. Vol. 11, 1895, X1 + 983 pp.

Melin, D. 1930. "Contributions to the study of the Theory of Selection 1". Zool. Bidr. Uppsala, X111, pp. 87-104.

Mez, C. 1890. "Morphologische und anatomische Studien über die Gruppe der Cordiae". Engler's Bot. Jahrb. X11, pp. 526-588.

Miehe, H. 1911. "Ueber die javanische Myrmecodia und die Beziehung zu ihren Ameisen". Biol. Centralbl. XXX1. pp. 733-738.

Möbius, M. 1925. "Versuch zur Erklarung der Ameisenpflanzen". Flora, CXV111 and CX1X. pp. 393-

Möller, A. 1893. "Die Pilzgarten einiger sudamerikanischer Ameisen". Bot. Mitt. aus den Tropen, Jena. V1. pp. 1-127.

Nieuwenhuis von Üxküll-Güldenbrandt, M. 1907. "Extraflorale Zuckerausscheidungen und Ameisenschutz." Ann. Jardin Bot. Buitenzorg. XX1. pp. 195-328.

Pearson, H. H. W. 1902. "On some species of Dischidia with double pitchers". Journ. Linn. Soc. London. Botany, XXXV, No. 245, pp. 375-390.

Rettig, E. 1904. "Ameisenpflanzen-Pflanzenameisen". Beih. z. Bot. Centralbl. XV11. pp. 89-122.

Ridley, H. N. 1910. "Symbiosis of ants and plants". Ann. of Bot. XX1V. pp. 457-483.

Rodway, J. 1894. "In the Guiana forest: Studies of nature in relation to the struggle for life". London, XX111 + 242 pp. (2nd. Edit. 1911).

Schimper, A.F.W. 1888. "Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika". Botan. Mitt. aus den Tropen, Jena. 1. pp. 1-95.

1898. "Pflanzengeographie auf Physiologischer Grundlage". Jena XV111 + 876 pp. (English Trans. Oxford. 1903).

Schumann, K. 1888. "Einige neue Ameisenpflanzen". Pringsheim"s Jahrb. Wiss. Bot. X1X. pp. 357-421.

1891. "Ueber afrikanische Ameisenpflanzen". Ber. Dtsch. Bot. Ges. 1X. pp. 54-72.

1902. "Ameisenpflanzen". Gartenflora, L1. pp. 95-101.

Shelford, R.W.C. 1916. "A Naturalist in Borneo". London. XXV11 + 331 pp.

Spruce, Rich. 1908. "Notes of a botanist on the Amazon and Andes". Edited by A.R. Wallace. London. vol. 1. L11 + 518 pp; Vol. 11. X11 + 542 pp.

Treub, M. 1883. "Sur le Myrmecodia echinata". Ann. Jardin Bot. Buitenzorg, 111. pp. 129-157.

1888. "Nouvelles recherches sur le Myrmecodia de Java". Ann. Jardin Bot. Buitenzorg. V11. pp. 191-212.

Ule, E. 1901. "Ameisengarten im Amazonasgebiet". Engler's Bot. Jahrb. XXX. Beibl. No. 68. pp. 45-52.

1905. "Wechselbeziehungen zwischen Ameisen und Pflanzen". Flora XC1V. pp. 491-497.

1906. "Ameisenpflanzen". Engler's Bot. Jahrb. XXXV11,3,pp. 335-352.

Warburg, O. 1892. "Ueber Ameisenpflanzen". Biolog. Centralbl. X11. pp. 129-142.

Wheeler, W. M. 1921. "A new case of Parabiosis and the'Ant-Gardens'of British Guiana". Ecology. Brooklyn. 11. pp. 89-103.

Wheeler, W.M. and Bequaert, J.C. 1929. "Amazonian Myrmecophytes and their Ants". Zool. Anz. Leipzig. LXXX11. pp. 10-39.

Yapp, R.H. 1902. "Two Malazan 'myrmecophilous' ferns, Polypodium (lecanopteris) carnuosum (Blume), and Polypodium sinuosum Wall". Ann. of Bot. XV1. pp. 185-231.