V.—THE ANATOMY OF CERTAIN PLANTS FROM THE BELGIAN CONGO, WITH SPECIAL REFERENCE TO MYRMECOPHYTISM

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Introduction

In examining a dried specimen of the myrmecophytic *Vitex Staudtii* Guerke collected by Lang and Chapin at Medje in the Belgian Congo, I was impressed by the close correlation between the distribution of the lateral cavities (supposed excavations) and the phyllotaxy of the plant. Through the courtesy of my colleague, Professor Wheeler, to whom the material had been sent by the collectors, I secured the opportunity of sectioning nodes and internodes of portions of the specimen and of studying their anatomical structure. So many features of unusual interest were encountered that it seemed advisable to study in detail the anatomy of other myrmecophytes from tropical Africa. All of the available material of ant-inhabited species of *Sarcocephalus*, *Barteria*, *Plectronia*, and *Cuviera* secured by Dr. Bequaert and Messrs. Lang and Chapin was very kindly turned over for my use. The myrmecodomatia of these genera proved to be fully as interesting as those of *Vitex*. Indeed, in so far as the anatomy of the host plants is concerned, the African myrmecophytes are even more remarkable than the much discussed *Acaciæ*, *Cecropiæ*, and *Myrmecodiæ* and are specially significant in any general consideration of myrmecophily.

Minute Anatomy of African Myrmecophytes
Vitex Staudtii Guerke[1]

The taxonomy and general gross morphology of this verbenaceous liana are described by Dr. Bequaert on pages 447-452. The plant exhibits a typical decussate phyllotaxy. In other words, pairs of opposite leaves alternate with each other at right angles, resulting in four vertical rows or orthostichies of leaves. As is frequently the case in plants having this type of phyllotaxy, the stems are four-sided and quadrangular, each side corresponding to one of the orthostichies of leaves. At each node there are two circular apertures which are located at approximately the same level on opposite sides of the stem and midway between the leaf-scars or points of attachment of the leaves (Fig. 88e). These orifices, which serve as exit holes for the ants, shift their position from one pair of opposite sides of the stem to the alternating pair at each succeeding internode.

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[1]The following account of the anatomy and histology of this creeper is based upon the study of material (No. 743) collected by Lang and Chapin at Medje, July, 1914.

When the stem is split open it is found to be hollow. The central cavity is continuous from internode to internode, but is considerably constricted just above each node by a thicker peripheral layer of medullary tissue (Fig. 88, *A–A*). In addition to the nodal apertures which communicate with the exterior, there are numerous lateral internodal cavities which perforate the xylem and end blindly just under the bast. They are arranged symmetrically, one over the other, in longitudinal rows subtending the nodal apertures (Fig. 88*l*). In other words, there is an obvious and close correlation between the distribution of the lateral cavities and the phyllotaxy of the plant.

In specimens which are inhabited by *Viticicola tessmanni* (Stitz) Wheeler, the conditions described above are characteristic of all portions of the stems and branches having fully elongated internodes. Only during the earlier stages in the differentiation of the nodes and internodes —in relatively close proximity to the growing-points or apical meristems —are they filled internally with medullary tissue and devoid of lateral cavities. The longitudinal and lateral cavities are also absent in very young plants that are not inhabited by ants. Such facts as these suggest that the central cavities and their bisymmetrically arranged lateral ramifications are excavated by the ants, which leave the supernodal constrictions or projecting rings of medullary tissue to separate the broods and prevent them from falling downward into the lower internodes.

In his field studies of *Vitex Staudtii*, Dr. Bequaert was unable to find any external evidences of preformed structures like the "prostomata" of *Cecropia*, described by Fritz Müller (1880–81), Schimper (1888) and others, which might account for the curiously symmetrical arrangement of the nodal apertures and lateral internodal cavities; nor was he able to find any clue to the functional significance of the latter. They are not used as receptacles for eggs, larvæ, or pupæ, nor do they contain coccids or other organisms. The only explanation that suggested itself was that they might be constructed for purposes of aëration. This suggestion is negatived, however, by the structure of those portions of the "bark" which cover the outer ends of the supposed lateral excavations. There are no lenticels or patches of aërenchyma suitably located, through which air might readily penetrate into the interior. On the contrary, the overlying tissues are compact and devoid of conspicuous intercellular spaces, and, in old stems, there are thick disks of impervious sclerenchyma situated just opposite the ends of the lateral cavities (Pl. XXXII, fig. 4).

Lateral Cavities

In stout, dry stems and branches of *Vitex Staudtii*, the lateral cavities appear superficially to be galleries or pits excavated in the woody portion of the "central cylinder," or stele. As is shown in Pl. XXXII, fig. 4, they perforate the xylem and end blindly on a general level with the cambium. However, a more detailed and critical study of the histology of the tissues figured in this photomicrograph indicates conclusively that the cavities are not mere tunnels in the normal xylem, since there is no fringe of chewed and broken prosenchyma such as occurs in galleries excavated by wood-boring insects. The outer two-thirds of the cavity are jacketed by the remains of a layer of very thin-walled, unlignified cells (*TPa*). In the xylem this layer rests upon heavily lignified, thick-walled parenchyma (*LXmPa*) which, in turn, merges more or less abruptly into prosenchyma (*XmPr*) (Pl. XXXII, fig. 3). That these layers were not formed subsequent to the excavation of a cavity in the prosenchyma is shown by the fact that there is no unconformity—torn or broken libriform fibers—between the parenchyma and surrounding prosenchyma.

What, then, is the mode of formation of the lateral cavities? Are they preformed structures or galleries excavated from a pre-existing core of delicate tissue? The section, illustrated in Pl. XXXIII, fig. 1, which was made from a freshly cut stem preserved in alcohol is of considerable interest in this connection. The soft tissues are *in situ* and have not contracted and collapsed as in preparations made from dried specimens. The lateral cavity does not extend to the general level of the surface of the woody cylinder, but its convex end subtends a plug of soft tissue (*CT*) which projects into the xylem. The inner portion of this intruding mass of unlignified tissue is jacketed laterally by an extension of the layer of thin-walled, unlignified cells (*TPa*) previously mentioned, which resemble in size, shape, and orientation those of the adjoining layer of heavily lignified xylem-parenchyma (*LXmPa*). Externally, the central core is constricted more or less by the phloem and cortex, into which it gradually merges. Since its outer margin is somewhat convex and its inner surface is concave, it forms a roughly dome-shaped layer of considerable thickness. Dark-colored, elongated, conducting cells, ramifying from the phloem (*Pm*), proliferate through it, and, as is shown in Pl. XXXIII, fig. 2, the thin-walled isodiametric cells which form its ground mass are arranged more or less symmetrically in radiating rows. This is particularly true of its inner portion (*NL*), where the cells are very much smaller and of more uniform size and shape (Pl. XXXIII,

fig. 4). In examining the photomicrographs, it should be noted that the concave inner margin of this intruding core of delicate, unlignified tissue is irregularly serrate (Pl. XXXIII, figs. 2 and 4) and shows unmistakable evidences of having been gnawed by the ants. Small chunks of tissue have been nipped out of the surface, leaving a fringe of torn and injured cells. This suggests that the lateral cavities are not natural gaps in the woody portion of the central cylinder but are galleries excavated by the ants in peculiar cores of delicate, unlignified tissue, that are symmetrically distributed in certain radii of the stem.

The question presents itself, accordingly, as to whether these parenchymatous areas of the xylem are normal features in the anatomy of *Vitex Staudtii* or traumatic structures produced by the ants. They have the appearance of abnormalities and resemble certain complex zoöcecidia or so-called prosoplasmatic galls, with their histological differentiation into "nutritive," "mechanical," and "conducting" tissues. The similarity becomes very striking indeed when these peculiar structures are studied microchemically. The cells—septate libriform fibers and parenchyma—of the normal xylem are packed with starch (Pl. XXXIII, figs. 1 and 3) and are separated from the core of thin-walled tissue by the layer of thick-walled, heavily lignified parenchyma corresponding to a mechanical layer, which is devoid of starch, as is the thin-walled unlignified parenchyma which adjoins it. The dome-shaped, central core of soft tissue is abundantly supplied with proteins and fats, which reach their highest concentration in the cloudy protoplasts of the small, regularly arranged cells of the inner zone (Pl. XXXII, fig. 5). In stout stems the cap or disk of sclerenchyma, which is formed by the periderm and overlies the soft core of unlignified tissue (Pl. XXXII, fig. 4), corresponds to a second mechanical layer. It is evident, accordingly, that in the tissues which surround the lateral cavities there are the equivalents of a "starch layer," a "protein-fat," or "nutritive" layer, two "mechanical" layers, and a ramifying system of conducting cells. As in certain insect galls,[1] the starch and protein-fat containing tissues are separated by a layer of heavily lignified cells, and the second, mechanical or "protective" layer is situated near the exterior. However, in view of the fact that ants are not known to produce gall-heteroplasias, particularly of this highly differentiated and structurally complex type, more critical evidence is required before these structures can safely be considered to be of traumatic origin and due solely to the activity of the ants.

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[1]Compare cynipid and other prosoplasmatic zoocecidia described by Houard (1903), Küster (1903, 1911), Cosens (1912), and others.

I have already stated that the lateral cavities do not contain coccids or the larvæ of gall-making insects; this is true of young as of old, stout stems and branches. Furthermore, the tissues in question do not appear to contain bacteria or other micro-organisms. In very young, tender stems, just subsequent to the formation of the longitudinal central cavity, the flat sides of the stele, or so-called fibrovascular cylinder, are prosenchymatous and devoid of gaps or oval patches of delicate tissue, and the peripheral layer of medullary tissue is homogeneous and entire (Pl. XXXII, fig. 2). At a little later stage in the differentiation of the internodes, the lateral cavities make their appearance. Macroscopic and microscopic studies of the tissues in the interior of such internodes reveal very clearly the mode of origin of the oval lateral pits. Patches of the medullary tissue are ripped and torn away and the prosenchyma is perforated, revealing the cambium. The exposed portion of the latter divides actively, producing callus, which projects toward the interior of the stem (Pl. XXXIV, fig. 2). With further increase in the size of the stem, the cavities, which are somewhat irregular at first with jagged margins, are enlarged by the removal of additional elements of the medulla and prosenchymatous xylem and are smoothed till they finally assume their characteristic symmetrical, oval outlines (Pl. XXXII, fig. 3). These facts indicate very clearly not only that the lateral cavities are excavated by the ants, but that the peculiar tissues that surround them are abnormalities, comparable to zoöcecidia or heteroplasmatic galls.

Although the heteroplasias are relatively simple at their inception, they soon become complex and highly differentiated from the histological point of view. Thus, at first, there is merely a simple callus, which projects into a perforation in the prosenchymatous xylem. This is accompanied by more or less hypertrophy of the cells of the overlying cortex and a slight retardation in the development of the subepidermal periderm (Pl. XXXIV, fig. 2 and Pl. XXX, fig. 2). As growth proceeds, other structural abnormalities make their appearance. Owing to traumatic stimuli, the peripheral layer of meristematic cells of the cambium, adjoining the callus, ceases to form prosenchymatous xylem and lays down thick-walled, heavily lignified parenchyma next to the prosenchyma and thin-walled, unlignified tissue next to the callus. As the mass of the callus increases, extensions of the phloem proliferate through it, accelerating a flow of nutritive substances to its innermost portions. When the overlying periderm is differentiated, it remains for a time unmodified or only slightly modified in structure (Pl. XXXIII, fig. 1),

but later forms a disk of very dense, heavily lignified tissue, or scleren-chymatous cap, opposite the central core of delicate cells (Pl. XXXII, fig. 4). As the woody cylinder increases in diameter, the ants continu-ally, *i. e.*, at relatively frequent intervals, excavate the inner margin of the intruding mass of callus, for if they do not do so the lateral cavities become occluded by wound-wood. Such occluded galleries are of com-mon occurrence, particularly in long internodes having very numerous heteroplasias and small broods.

The next question to be considered then is, why are these zoöcecidia so symmetrically arranged in obvious correlation with the decussate phyllotaxy of the plant? Pl. XXX, fig. 1 illustrates a transverse section of a young internode, cut just ABOVE a node (at the level *A–A* of Fig. 88). The four sides of the quadrilateral stem are histologically similar, with one notable exception. The vessels or principal water-conducting pas-sageways are largely concentrated in one pair of opposite sides of the stele. A similar condition is shown in Pl. XXX, fig. 2, a transverse section cut just BELOW the node (at the level *B–B*, Fig. 88), but the vessels in this case are aggregated in the alternating pair of sides. In other words, the principal water-conducting passageways in each inter-node are largely confined to those sides of the stele which are to pass out to the leaves at the next (higher) node. Therefore, their orientation changes at each succeeding internode in accordance with the decussate phyllotaxy of the plant. As shown in Pl. XXX, fig. 2, the lateral cavities are excavated in the sides of the stele which are poorly supplied with vessels. Furthermore, they are located in those portions of the xylem which are devoid even of a narrow fringe of small primary tracheæ (*PT*).

Why should the ants select these radii of the stem for the construc-tion of the lateral pits? Of course, the breaking of the conduits would certainly interfere with the normal flow of water to the leaves, and, inas-much as in vines and lianas the area of water-conducting tissue is rela-tively small in proportion to the area of transpiring leaf-surface, this might affect the normal physiological processes of the plant and even lead to the drying up of the leaves. It seems probable, however, that the ants avoid the vessels because when the conduits are ruptured there is an excessive flow of water. That the cambia on the four sides of the stem are equally capable of producing the hyperplasias, is indicated by the fact that when the ants make an excavation in the wrong surface, as occasionally happens, it results in the formation of a heteroplasia which resembles those that occur so abundantly in the alternating pair of sur-faces.

Exit Apertures

In stout stems the inner portions of the exit holes resemble structurally those of the lateral pits which subtend them. The prosenchymatous xylem is jacketed by thick-walled, lignified parenchyma which is covered in turn by a layer of thin-walled, unlignified tissue. The outer surface of the xylem surrounding the exit gallery, however, is depressed considerably below the general level of the woody cylinder (Pl. XXXIV, fig. 1). In this depression rests a peculiar ring of sclerenchyma (Pl. XXXIV, figs. 1 and 3) which extends to the outer surface of the stem and usually projects considerably beyond it, so that the nodal apertures have externally an embossed or crater-like profile. These rings of extremely dense, tough tissue make their appearance in young stems and undoubtedly tend to prevent the cambium and cortex from forming lateral callus which would seal the exit hole unless periodically removed by the ants.[1] Similar structures may be formed in the internodal portions of the plant whenever, as occasionally occurs, one of the lateral galleries is extended beyond the cambium, through the cortex and epidermis, to the exterior of the stem. Under these circumstances the usual sclerenchymatous disk (Pl. XXXII, fig. 4) is replaced by a projecting ring of sclerenchyma (Pl. XXXIV, fig. 1).

I have already called attention to the bisymmetrical arrangement of these nodal apertures and their obvious relation to the decussate phyllotaxy of *Vitex Staudtii*. At each node there are two exit holes excavated on opposite sides of the stem and at approximately the same level (Fig. 88). It is interesting to note in this connection that in the verbenaceous myrmecophyte, *Clerodendron fistulosum*, described and figured by Beccari (1884–86), the nodal apertures[2] are located just below the points of attachment of the leaves, in the alternating pair of surfaces of the stem. This striking contrast in the location of the exit holes in the two myrmecophytes is due apparently to differences in their nodal and internodal anatomy. In *Vitex Staudtii* two entire sides of the stem pass out into the pair of opposite leaves at the node. These sides—"leaf traces" —which are considerably narrower than the alternate pair (Pl. XXX, fig. 2) become more and more abundantly supplied with vessels in the vicinity of the node. With the passing out of the leaf-traces, leaving two large gaps in the stele, there is an abrupt transition in the remaining sides of the stele from xylem that is nearly devoid of vessels to woody

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[1] In a number of other myrmecophytes that I have studied the exits or entrances soon become blocked by callus and ultimately by wound-wood unless kept open by the ants.

[2] Schimper (1888) questions Beccari's statement that these apertures arise spontaneously and considers that they are excavated by ants.

tissue that is crowded with water-conducting passageways. Therefore, the most favorable situations for the location of the nodal apertures are to be found midway between the points of attachment of the leaves and just below the level where these structural transitions occur. In the stems of certain species of *Clerodendron*, on the other hand, the elements of the xylem are differentiated and distributed in such a manner that the "prostomata" subtend the bases of the leaves.

The gaps left in the woody cylinder by the exit of leaf-traces are filled with very delicate, soft tissue. *A priori*, it would seem as if these gaps would be the most favorable places for the excavation of the exits. It should be noted, however, that if they were so utilized there would inevitably result a destruction of the axillary buds and the formation of lateral branches be prevented. In *Vitex Staudtii*, although the ants occasionally remove a portion of the tissue, I have never seen a node in which they had cut their way through to the exterior. Yet, as soon as the buds form branches, the cavities in the latter are found to communicate freely with those of the main axes. From the point of view of insect behavior, it would be extremely interesting to discover whether there are structures or substances in the buds which prevent their destruction by the ants.

Origin of the Central Cavities

Many of the earlier investigators assumed that the central chambers of various myrmecodomatia are excavated by ants. Thus, Rumphius (1750) and others considered that the anastomosing galleries in the "pseudobulbs" of *Myrmecodia* and *Hydnophytum* are constructed by ants. There is a considerable element of danger, however, in making hasty generalizations in regard to the origin of these structures. Forbes (1880), Treub (1883), and others have shown that the domatia of *Myrmecodia* and *Hydnophytum* occur normally in plants from which ants are entirely excluded. Furthermore, it is well known that plants, both herbaceous and arborescent, having hollow internodes are widely distributed in both temperate and tropical regions.

It has been stated that the stems of very young seedling plants of *Vitex Staudtii*, which are not inhabited by *Viticicola*, are filled with medullary tissue, whereas those of older plants, which are occupied by the ants, are hollow except in the vicinity of the growing points. This might be considered to indicate that the domatia are excavated by *Viticicola*. It must be admitted, however, that evidence of this character is purely circumstantial and not necessarily conclusive. Hollow internodes

may be present in large, vigorous adult shoots when they are entirely absent in smaller stems, such as are frequently formed during the earlier stages in the ontogeny of the plant or under unfavorable growth conditions. Furthermore, in examining herbarium material of other representatives of this genus, I find that, although certain species possess solid stems, others normally have well-developed central cavities in their core of medullary tissue (Pl. XXXI, fig. 1). The structure of the delicate, immature internodes of ant-inhabited specimens of *Vitex Staudtii* is of interest in this connection. Pl. XXXII, fig. 1 illustrates a transverse section of such an internode.cut a relatively short distance behind the terminal growing-point. The medulla is not homogeneous but consists of an oval central core of very large, thin-walled cells and a peripheral layer of denser medullary tissue, which is richly protoplasmic. As the stem increases in diameter the oval core of delicate tissue shrivels up and is trimmed away by the ants leaving the oval cavity shown in Pl. XXXII, fig. 2. From the point of view of this histological evidence, it seems probable that in *Vitex Staudtii* there is an inherent tendency towards the formation of hollow stems and branches. Whether the ants accelerate the formation of the central cavities, as has been shown by Fiebrig (1909) to be the case in *Cecropia*, can only be determined by careful field observations.

Cuviera

A number of species of the African, rubiaceous genus *Cuviera* are myrmecophytic and characterized by having elongated, spindle-shaped swellings on the branches (Figs. 99 and 100) which are inhabited by ants.[1] Two lots of these myrmecodomatia, one collected by Dr. Bequaert at Stanleyville, March 8, 1915 and the other (No. 1031) by Messrs. Lang and Chapin at Kunga near Malela, July, 1915, were sent to me for anatomical study. The former, occupied by *Crematogaster africana* subspecies *laurenti* variety *zeta* (Forel), were obtained from *Cuviera angolensis* Hiern; the latter, inhabited by *Crematogaster impressiceps* variety *frontalis* Santschi, from an unidentified species of *Cuviera*.

The myrmecodomatia of the two species are similar and differ only in certain minor morphological and histological details. Externally, those of *Cuviera angolensis* are shorter, slimmer, and of a deep olive green color, whereas the others are longer, stouter, and of a reddish green color.[2] The color differences are due largely to differences in the internal

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[1] See Schumann (1891).
[2] In making these comparisons I am dealing with material preserved in alcohol.

distribution of a translucent, amorphous, amber-colored substance commonly referred to as "tanniniferous" or "resiniferous," which occurs normally in many of the Rubiaceæ. As is shown in Pl. XXXV, fig. 1, there is a considerable concentration of this amber-colored substance in the subepidermal and other cortical cells of the unidentified species of *Cuviera*, which gives to the branches their reddish tinge. In *C. angolensis*, on the other hand, the cortex and bast are relatively free from it (Pl. XXXV, figs. 2 and 3; Pl. XXXVI). The structure and shape of the core of medullary tissue is not the same in the two species. In the former (Pl. XXXV, fig. 1), the cells which contain the amber-colored substance are aggregated in the center of the more deeply lobed medulla, whereas in the latter (Pl. XXXV, fig. 2) they are diffused, with a peripheral row scattered along the inner margin of the stele.

Mode of Origin of the Myrmecodomatia

As has been shown by Dr. Bequaert (Part IV, p. 490), the myrmecodomatia are not abnormalities produced by ants or gall-forming organisms. They are preformed, localized, hollow hypertrophies of the branches that become occupied by ants, or occasionally by the larvæ of certain beetles, after they have become fully differentiated. This is shown very clearly by the structure of swollen branches which have no entrance holes and are entirely devoid internally of insects or other organisms during the various stages of their "ontogeny." Pl. XXXVI, fig. 1 illustrates a transverse section of the swollen, lower portion of a young, tender internode. The cortex, stele, and medulla are already clearly outlined, but their finer histological details are still in process of differentiation. The pith is not homogeneous, as is the case in the unswollen, upper portion of the internode, but consists of a large central core of succulent pulp and a peripheral layer of denser tissue. Furthermore, it is evident that the differentiation of the so-called fibrovascular cylinder is not proceeding uniformly, since two opposite sides of the stele are considerably thicker than the intervening pair. As the lower part of the internode becomes more and more hypertrophied, the juicy delicate tissue in its interior gradually collapses and dries up; except for a fringe of thin-walled cells, filled with the amber-colored, hyaline substance, which jacket the inner margin of the peripheral layer of thick-walled medullary tissue (Pl. XXXVI, fig. 2).

Entrance Holes

Although the circular apertures, through which the ants gain access
to the interior of the swollen internodes, are not so regularly arranged as
in *Vitex Staudtii*, yet they 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 inter-
node. This is determined apparently by the structure of the walls of the
myrmecodomatia. As is shown in Pl. XXXV, fig. 3 and Pl. XXXVI,
fig. 1, the four sides of the swollen portion of the branch are not similar
either in size or in thickness. The ants almost invariably make their
primary excavations in the thin side of the stem which has the widest
surface. Therefore, since the position of this surface is closely related
to the decussate phyllotaxy, the orientation of the entrance holes shows a
similar correlation.

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, and before the cambium
has formed numerous prosenchymatous elements in the thinner sides of
the swollen internodes.

Lateral Excavations and Heteroplasias

As shown in Figs. 99*b* and 100*a-b*, the myrmecodomatia of *Cuviera*
are characterized internally by a number of elongated or oval pits which
are located in the thinner sides of the branch. These depressions, which
are arranged in one or two longitudinal rows, or more irregularly scat-
tered, are commonly occupied by coccids of different ages and sizes.[1]
In certain myrmecodomatia each pit contains a coccid which more or
less completely fills it, whereas in others only two or three of the pits
are so occupied, or the coccids may be entirely absent.

When studied microscopically, these pits are found to contain
growths of thin-walled callus (Pl. XXXV, fig. 3; Pl. XXXVII, fig. 2)
which recall the dome-shaped callus formations that occur in the lateral
galleries of *Vitex Staudtii*. As in the latter, the cells are arranged in
radiating rows but, instead of containing cloudy, opaque protoplasts,
are filled with the golden yellow, or reddish brown, hyaline substance
which occurs normally in certain cells of the cortex, phloem, xylem, and
medulla. In addition, it may be noted that the prosenchymatous margin

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[1]The coccids in *Cuviera angolensis* have been identified by Newstead as *Pseudococcus citri* variety
congoensis Newstead.

of the xylem is not jacketed by two clearly defined layers of parenchyma, and there is no elaborate, ramifying system of conducting cells (Pl. XXXVII, fig. 2).

The structure of these heteroplasias, as well as their entire absence in swellings which have not been occupied by insects, indicates that they are abnormalities produced by traumatic stimuli.   The question presents itself, accordingly, are they due to the activities of the ants or the coccids? That they serve as food-reservoirs for the coccids is shown by the fact that the sucking mouth-parts of the latter are embedded in the callus.   The torn and chewed inner margin of the heteroplasias (Pl. XXXVII, fig. 1) suggests, however, that these layers are also fed upon by the ants. Furthermore, the pits or depressions originate as excavations in the thinner walls of the domatia and not by the collapse of soft tissue or the retardation of the growth of tissues underlying the coccids.   Since the cells of the peripheral layer of medullary tissue and the first-formed elements of the prosenchymatous xylem are relatively tough and thick-walled at the time when the excavations are started, they must have been made by insects with strong mandibles and not by the delicate sucking mouth-parts of the coccids.   In this connection, it should be emphasized in passing that all of the myrmecodomatia examined contained the lateral pits and heteroplasias regardless of the presence or absence of the coccids. As in *Vitex Staudtii*, the ants evidently cut through to the cambium and induce the formation of a nutritive callus before the stele becomes considerably thickened.

"Fungus Gardens"

As has been stated previously, the internal cavities of hypertrophied branches which have no entrance apertures are entirely devoid of parasitic or saprophytic organisms. The walls of the myrmecodomatia, on the contrary, form the substratum for a more or less luxuriant growth of fungi.   In recently occupied cavities, which are jacketed by a layer of cells containing the amber-colored substance, scattered aërial hyphæ project into the interior from all sides (Pl. XXXVII, fig. 3).   In the case of the domatia of the unidentified species of *Cuviera*, which contain numerous ants, the hyphæ and amber-colored substratum have been more or less cleanly gnawed away except at the two ends of the spindle-shaped cavity (Pl. XXXVIII, fig. 1) where there are dense growths of delicate, white hyphæ, resembling "ambrosia."   As shown in Pl. XXXVIII, fig. 4, there is a considerable layer of detritus between this crop of aërial hyphæ and the basic substratum of medullary tissue.

When analyzed microscopically, the detritus is found to consist largely of the more or less disintegrated castings from the infrabuccal chambers of the ants and to contain numerous nematodes (Pl. XXXVIII, fig. 3). The hyphæ radiate through this layer in all directions and penetrate into the underlying medullary cells. In the myrmecodomatia of *C. angolensis,* which contain relatively few ants, there is a similar terminal concentration of hyphæ, but it is less conspicuous, owing to the fact that the lateral walls of the cavities have been less thoroughly scarified.

Plectronia species *A*

Among the specimens turned over to me for anatomical study were some myrmecodomatia, preserved in alcohol, which were collected by Dr. Bequaert near Stanleyville, March 6, 1915. They were inhabited by *Engramma kohli* Forel and were collected from an unnamed species of the rubiaceous genus *Plectronia,* referred to as species *A* in Part IV (p. 474).

The myrmecodomatia of this plant resemble those of *Cuviera* in that they are preformed, localized, hollow swellings of the branches which are occupied by ants (Fig. 96). Sections of the normal and abnormal portions of the branches are illustrated by photomicrographs on Pl. XXXIX. As in the case of *Cuviera angolensis* (Pl. XXXV, figs. 2 and 3), the pith in the former regions is homogeneous, whereas in the latter portions it is heterogeneous, consisting of a succulent central pulp, which collapses, and a peripheral layer of denser medullary tissue. Two opposite sides of the swollen branch are considerably thinner than the alternate pair, and the differentiation of the cambium and fibrovascular tissues is retarded in them. The ants pierce one of these thin walls and scarify its inner surface, as well as that of the opposite side. From these injured surfaces and from the margins of the irregularly shaped apertures heteroplasias originate, which superficially resemble those that occur in *Cecropia* under somewhat similar circumstances (Pl. XL, fig. 1). As shown in Pl. XL, fig. 2, the heteroplasias consist of two distinct tissues— a central core of thick-walled, heavily pitted parenchyma, that is packed with starch, as is the parenchyma of the normal and abnormal xylem; and an outer layer of thin-walled, isodiametric cells, which are filled with an amber-colored, hyaline substance such as occurs in the heteroplasias of *Cuviera.* The torn and chewed inner margin of this layer indicates that it is eaten by the ants. Furthermore, in a number of the myrmecodomatia small coccids were found attached to this callus-tissue by their proboscides.

In addition to the myrmecophytes that have been described in the preceding pages, and of which there was an abundance of well-preserved material suitable for anatomical study, there are four others of which unfortunately only fragmentary material is available. However, in view of the fact that more abundant and better preserved specimens cannot be obtained in the immediate future, it seems desirable to call attention to certain features of these plants, upon which some light is thrown by the evidence at hand.

Plectronia Laurentii De Wildeman

The myrmecodomatia of this interesting plant have been described and figured by De Wildeman (1905–07) after É. Laurent's notes and by Kohl (1909). Additional notes upon their gross morphology are given by Dr. Bequaert (p. 471; Fig. 95a and b). My own observations are based upon the study of two dried myrmecodomatia, collected by Dr. Bequaert near Stanleyville, March 6, 1915, which contain coccids and *Crematogaster africana* subspecies *laurenti* variety *zeta* (Forel).

The myrmecodomatia are preformed, more or less pronounced hollow swellings of the stems and branches, of the two general types figured on Pl. XLI. The internal cavities originate apparently by the falling away of the central succulent portion of the heterogeneous medulla. As in the case of the previously described myrmecophytic plants, 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 succeeding internode in correlation with the decussate phyllotaxy of the plant. The pits contain heteroplasias which resemble those of *Vitex Staudtii* in that their nutritive layers do not contain an amber-colored substance. Many of the coccids are attached to this tissue by their sucking mouth-parts. The zoöcecidia resemble those of *Vitex Staudtii* in the frequent occurrence of an outer cap of sclerenchyma, which is formed by a periderm opposite the delicate core of callus (Pl. XLI, fig. 2). The less quadrangular of the two myrmecodomatia examined by me contains "fungus gardens" at the two ends of its spindle-shaped inner cavity, which closely resemble those that occur in *Cuviera*. However, in these domatia the substratum of thick-walled medullary tissue, upon which the gardens rest, does not contain an amber-colored substance. The parenchyma of the woody cylinder and the cells of the medulla, except those in the vicinity of the central cavity, are densely packed with starch.

Barteria fistulosa Masters and **B. Dewevrei** De Wildeman and Durand

The taxonomy and general gross morphology of these flacourtiaceous myrmecophytes have been discussed in detail by Schumann (1891), De Wildeman (1905–07), and by Dr. Bequaert on pp. 432–441. *B. fistulosa* is characterized by numerous hypertrophied, hollow, deciduous branches which are frequently more or less fasciated in appearance (Fig. 86), *B. Dewevrei* by hollow stems and branches of normal dimensions (Fig. 87).

The material that I have studied consists of several myrmecodomatia of *B. fistulosa* (No. 933), collected by Messrs. Lang and Chapin near Stanleyville, larvæ of *Pachysima æthiops* (F. Smith) (No. 747), removed from the myrmecodomatia of *B. fistulosa* at Medje, and a section of a hollow twig (No. 175) of *B. Dewevrei*, secured by Dr. Bequaert near Leopoldville. The myrmecodomatia of *B. fistulosa* contained *Crematogaster buchneri* subspecies *biimpressa* (Mayr) and *Pseudococcus citri* variety *congoënsis* Newstead; the hollow twig of *B. Dewevrei*, *Crematogaster (Atopogyne) africana* variety *schumanni* (Mayr), and *Lecanium (Saissetia) barteriæ* Newstead.

Pl. XLII, fig. 1 illustrates a transverse section of the normal, unswollen, basal portion of a deciduous branch of *B. fistulosa*. The pith is homogeneous and consists of compact, relatively thin-walled parenchyma. The fibrovascular cylinder or stele is well developed and of normal structure. In the hypertrophied portion of the branch or myrmecodomatium, on the contrary, the medulla is heterogeneous and the stele is feebly developed and broken up into separate strands or bundles (Pl. XLII, fig. 2). A core of succulent pulp has evidently collapsed except for a layer of thin-walled cells which jacket the cavity and are filled with an amber-colored substance such as occurs in *Cuviera* (Pl. XXXVI, fig. 2). The amber-colored substance also occurs in cells which are scattered through the peripheral layer of denser medullary tissue, and in the subepidermal cells of the cortex. É. Laurent (1903–04; see De Wildeman, 1905–07) and Kohl (1909) found lateral pits or depressions in the walls of the myrmecodomatia of *Barteria fistulosa*, many of which were occupied by coccids. These structures are not present in the myrmecodomatia that I have sectioned and the coccids are attached to various portions of the walls of the domatia by their probascides. It should be noted, however, in this connection, that my material consists entirely of young, succulent branches in which processes of secondary growth are still in their incipient stages. The depressions are probably excavated in older or more woody myrmecodomatia.

A transverse section of the branch of *B. Dewevrei* (Pl. XLIII, fig. 1) resembles a similar section of the normal, unswollen portion of a deciduous branch of *B. fistulosa* (Pl. XLII, fig. 1). It differs from it, however, in two important features. The pith is heterogeneous and the internal cavity, which serves as the domatium of the ants, is jacketed by a layer of thick-walled, medullary parenchyma containing an amber-colored, hyaline substance. Furthermore, one side of the myrmecodomatium is much thinner than the others and is nearly devoid of vessels. The entrance apertures are commonly located in this wall, as are rows of depressions or oval pits (Fig. 87*d*). The latter and the heteroplasias which partially fill them (Pl. XLIV, fig. 2) recall those that occur in *Cuviera* (Pl. XXXVII, fig. 2). The large, thin-walled cells of the callus are filled with an amber-colored, hyaline substance, which occurs normally in many of the parenchymatous cells of the medulla and stele. The coccids evidently feed on the substances in these callus-formations, for their sucking mouth-parts are embedded in them. 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.

Sarcocephalus species

Among the myrmecophytes described by Dr. Bequaert is an interesting species of the rubiaceous genus *Sarcocephalus* (p. 460; Fig. 92). Unfortunately, the only available structural material of this plant consists of a dried section of a single myrmecodomatium (No. 161) which was collected at Masongo between Walikale and Lubutu. It was inhabited by *Crematogaster (Atopogyne) africana* subspecies *winkleri* variety *fickendeyi* (Forel) and coccids, which are identified by Newstead as *Pseudococcus crassipes* Newstead.

As shown in Pl. XLIII, fig. 2, this myrmecodomatium differs from the others that have been described in having four thin sides which alternate with four thick sides. Longitudinal rows of pits or grooves, which are more or less completed filled by callus-growths, are situated in these thinner walls. Numerous coccids are attached to these heteroplasias, so that when one looks through the hollow twig there are four rows of these insects hanging from the four corners of the quadrangular cavity. The heteroplasias resemble those of *Vitex Staudtii* and *Plectronia Laurentii*, since their cells do not contain a golden or reddish brown, hyaline substance; nor is the central cavity jacketed by a layer of cells which are filled with this material. The pith is heterogeneous and apparently once

contained a central core of succulent pulp, which has collapsed and has been removed by the ants.

SALIENT FEATURES OF AFRICAN MYRMECOPHYTES

Although these African myrmecophytes belong to three distinct orders (Parietales, Tubifloræ, and Rubiales) and to different growth forms (trees, shrubs, and lianas) they are fundamentally similar from the anatomical and histological points of view. In all, there is apparently an inherent tendency towards the formation of a heterogeneous pith, the central succulent portion of which collapses and dries up leaving an internal chamber or cavity. They are all characterized by similar peculiarities in the differentiation of their fibrovascular cylinders, which are more or less closely correlated with phyllotaxy. Certain sides or radii of the stele tend to be thinner, to contain fewer vessels, and to differentiate later than others. In *Cuviera, Plectronia, Sarcocephalus*, and *Barteria fistulosa*, the internal cavities and peculiarities in the differentiation of the medullary and fibrovascular tissues tend to be localized in certain shoots, or certain portions of the stems and branches, and are concomitants of more or less pronounced hypertrophies of these organs. In *Vitex Staudtii* and *Barteria Dewevrei*, on the other hand, in which these conditions are more generalized, there are no external indications of swellings or abnormal enlargements of the stem and branches.

All of these myrmecophytes differ from previously described extra-African myrmecophytic plants in the occurrence, within their myrmecodomatia, of excavations that contain peculiar callus-heteroplasias.[1] These traumatic structures, which are situated, like the entrance and exit apertures, in the thinner or evascularized sides of the myrmecodomatia, are arranged more or less symmetrically in relation to the phyllotaxy of the plants, and are formed by the young cambium and cortex when these tissues are exposed by the removal of the underlying cells of the medulla and xylem. Another unique feature of this group of myrmecophytes is the occurrence in the *Cuvieræ* and *Plectronia Laurentii* of "fungus gardens." Furthermore, with the exception of *Vitex Staudtii*, all of the African myrmecophytes are characterized by containing more or less numerous coccids.

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[1]Other myrmecophytes, upon further and more critical study, may be found to contain similar structures. The "stomatomes" of *Cecropia*, described and figured by Fritz Müller (1880–81) and H. von Ihering (1907), although not located in pit-like excavations, resemble to a certain extent the heteroplasias of the unidentified species of *Plectronia*.

The myrmecodomatia of the *Cuvieræ*, *Barteriæ*, and certain of the *Plectroniæ* resemble each other in being jacketed internally by layers of cells which are filled with an amber-colored substance. The large, thin-walled cells of the heteroplasias in these myrmecophytes are also characterized by being filled with this substance. The heteroplasias in *Vitex Staudtii*, *Plectronia Laurentii*, and the species of *Sarcocephalus*, on the contrary, are devoid of this hyaline substance.

FOOD OF TWIG-INHABITING ANTS

As is shown in the appended bibliography, a considerable number of investigators have devoted more or less attention to the study of myrmecophytism but, in spite of the significance attached to the supposed symbiotic relation between plants and ants, there is comparatively little reliable information concerning the feeding habits of the latter and the extent to which they are dependent upon the former for food. It is true that one finds in the literature many conclusions in regard to the general feeding habits of the ants, but these are frequently mere assumptions and are not supported by conclusive evidence. Even in the case of the much discussed "Beltian and Müllerian food-bodies" and extra-floral nectaries, although it has been definitely established that the former are collected and the latter frequently visited by the ants, there are no critical and detailed field observations or carefully planned experimental investigations which reveal the exact nutritional significance of these structures and the rôle that they play in the feeding of larvæ, queens, and various castes of workers.

Many writers assume that, because a tissue which contains carbohydrates or other possible nutrient substances, is excavated or gnawed by ants, it serves as an important reservoir of food for these insects. Thus, a number of investigators have concluded that the ants feed upon the fresh, succulent, or more or less collapsed and dried, medullary tissue of various myrmecophytes. For example, Belt (1874) states that in the "bull's-horn" *Acaciæ*, "the thorns, when first developed, are soft and filled with a sweetish pulp substance; so that the ant, when it makes an entrance into them, finds its new house full of food." Similarly, Fiebrig (1909) and H. von Ihering (1907) assume that in *Cecropia* the juicy pith of young internodes forms an important item of food in the diet of the *Aztecæ*. It should be noted, however, that in the absence of reliable collateral evidence, the mere fact that the medullary tissue is excavated or gnawed by the ants does not indicate necessarily that it is actually eaten by them, since it may be removed solely for the purpose of clean-

ing or enlarging the domatia. Thus, Fiebrig (1909) records having seen *Aztecæ*, in young internodes of *Cecropia*, busily engaged in excavating the medulla and casting the fragments out of the domatia through the subnodal apertures.

There is a similar uncertainty as to whether the more or less "pure cultures" of fungi, that grow upon the walls of ant nests, actually are fungus gardens, or are mats of weeds which are periodically trimmed away by the ants. Emery (1899), Lagerheim (1900), Ferdinandsen and Winge (1908), Farquharson (1914), J. S. B. Elliott (1915), Donisthorpe (1915), and others assume that various Formicidæ, other than the Attini, are fungivorous. These investigators base their conclusions upon one or more of the following lines of evidence: (1) the association of a particular fungus with a particular species of ant; (2) the occurrence of the fungus in "pure cultures"; (3) the cropping of aërial and other hyphæ by the ants; and (4) analogies with the remarkable fungus-growing and fungus-feeding habits of the attine ants. It must be admitted, however, that evidence of this character is not at all conclusive. Thus, the cropping of mycelia does not prove that a fungus is eaten by an insect. Miehe (1911) found localized, luxuriant growths of certain fungi in the pseudobulbs of *Myrmecodia* and *Hydnophytum*, but concluded that the hyphæ were cropped by the ants merely to prevent them from occluding or obstructing the galleries. The occurrence, in ant nests, of more or less pure cultures of fungi does not indicate necessarily that the mycelium is actually cultivated and eaten by the insects, since, as suggested by Perkins (1914), the mats of hyphæ may be purely adventitious. Furthermore, there is much uncertainty in reasoning from analogy with the highly specialized, phytophagous Attini that cosmopolitan, more or less omnivorous representatives of the Formicidæ are fungus-farmers.

A number of investigators assume that the coccids, which occur in so many myrmecophytes, are introduced into the myrmecodomatia by the ants and tended by them as "milch cows." For example, Belt (1874) states that in *Cecropia* the *Aztecæ* "do not obtain their food directly from the tree, but keep brown scale insects (Coccidæ)—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." Ule (1906) notes that most myrmecophytes contain coccids and assumes that they are brought into the domatia by the ants. É. Laurent (1903–04; see De Wildeman, 1905–07) and Kohl (1909) reach similar conclusions in regard to the coccids in *Barteria fistulosa*, and the latter infers that "im

Inneren ihrer Wohnungen geben sich die Ameisen fleissig mit der Schild-
läusezucht ab, in deren Exkrementen ihre hauptsächlichste Nahrung
besteht." Fiebrig (1909), on the contrary, believes that the coccids in
Cecropia "in keinem direkten Verhältnis zu diesen Ameisen stehen,"
and Dr. Bequaert (Part IV, p. 436) is of the opinion that the coccids find
their way into the myrmecodomatia of their own accord, just as they
do into other cavities (normal and abnormal) that are not inhabited by
ants.

It is difficult to observe the normal activities of ants in myrmeco-
phytes, even when living plants and insects are available. Therefore,
they must be studied in artificial nests or by indirect methods. Valuable
clues in regard to the feeding habits of other animals have been obtained
by analyses of feces or the contents of alimentary tracts. Unfortunately,
ants (imagines) take only fluids or semifluids into their crops and
stomachs. They do not masticate their food with their mandibles or
maxillæ. The act of feeding consists in lapping or rasping nutrient sub-
stances—which previously may have been dismembered or cut into
fragments of suitable sizes by means of the mandibles—with the rough-
ened surface of the protrusible tongue.

Meinert (1860) discovered that ants, like the social wasps,[1] have a
curious "mouth sac" which he considered to be a crop or "social
stomach." Although Meinert's conclusions were severely criticised by
Adlerz (1886), the latter was unable to determine the true function of this
infrabuccal chamber. In fact, Janet (1895, 1899) is the only student of
ants who has studied the function of the infrabuccal sac with any degree
of care. He demonstrated, by feeding experiments and by dusting ants
with various powders, that the sac acts as a receptacle for detritus—
which the imagines remove by means of their toilet organs from their
own bodies, from their progeny, and from their companions—and food-
residues. The latter substances may be of two distinct types: (1) coarse
fragments of animal or plant tissues, which adhere to the surfaces of
the ant during the process of cutting up or dismembering the food and
subsequently are swept into the sac; and (2) finely divided solids
rasped off by the tongue and segregated from the fluid or semi-fluid
substances that pass into the crop.

The material that accumulates in the infrabuccal cavity in the form
of a peculiarly moulded pellet, "corpuscule enroulé" of Janet, is finally
cast out as a useless residuum or fed to a larva (Pseudomyrminæ).

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[1]Previously investigated by Brants (1841).

Although it was by means of these infrabuccal pellets that H. von Ihering (1898) and Huber (1905) were able to throw so much light upon the origin of fungus gardens during the founding of new colonies of attine ants, I have not succeeded in finding a single investigator who has analyzed an extensive series of them in searching for clues concerning the feeding habits of ants.

The strongly hypocephalic larvæ of *Viticicola* and *Pachysima* are fed with pellets voided from the infrabuccal pockets of the workers. The pellets are inserted into a curious depression or pouch (trophothylax) which is located on the ventral surface of the larva close to its head. Owing to their relatively large size and dark color, these pellets are quite conspicuous and easily obtained from larvæ preserved in alcohol. Fortunately, I have been able to secure a large number of them and to compare them with pellets dissected from the heads of imagines. I have also dissected numerous workers of *Crematogaster africana* subspecies *laurenti* variety *zeta*, *C. impressiceps* variety *frontalis*, *C. buchneri* subspecies *biimpressa*, *C. (Atopogyne) africana* variety *schumanni*, and other ants which inhabit myrmecophytes, and have analyzed the contents of their infrabuccal pockets.

Food of *Viticicola tessmanni*

In his field studies of *Vitex Staudtii*, Dr. Bequaert was unable to secure any clue in regard to the chief sources of food of the ants, *Viticicola*, which are "obligatory" inhabitants of this myrmecophyte. The plants grow in wet, swampy regions and are not provided with food-bodies or extrafloral nectaries. Unless disturbed, the ants are not found running over the vegetation. They appear to remain, at least during the daytime, in the myrmecodomatia and, as shown by my colleague, Dr. Wheeler, (p. 108), seem to be structurally modified for their life in the dark, tube-like domatia of *Vitex Staudtii*. Their eyes are somewhat rudimentary for the group to which they belong and their body color is light yellowish brown, an unusual color in species of *Tetraponera*, to which *V. tessmanni* was originally referred.

I have shown at the beginning of this paper that certain of the tissues in the myrmecodomatia of *Vitex Staudtii* are abundantly supplied with nutrient substances. The cells of the outer portion of the peripheral layer of medullary tissue in young twigs are filled with starch, and the elements (parenchyma and libriform fibers) of the xylem are densely packed with grains of this carbohydrate. The "nutritive layer" of the gall-like heteroplasias, on the other hand, is rich in nitrogenous sub-

stances and fats. The ants gnaw this protein-fat layer, but, although they clean and smooth the interior of the domatia by removing more or less of the pith, they do not appear to cut through to the starch-containing cells, except at an early stage in the formation of the heteroplasias.

That the latter structures 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 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 (Pl. XLV, fig. 1) and bits of ant larvæ or triturated eggs (Pl. XLV, fig. 3).

Pellets of *Pachysima*

The pellets in the larval trophothylaces of *Pachysima æthiops* and *P. latifrons* are composed of substances obtained both from within and without the myrmecodomatia. Almost every pellet contains either a whole coccid larva (Pl. XLV, fig. 2), or one or more chunks of an adult coccid (Pl. XLIV, fig. 3). In addition, they have a relatively large admixture of fragments of medullary tissue, containing the amber-colored substance (Pl. XLV, fig. 6); aerial hyphæ from the walls of the domatia (Pl. XLV, fig. 5); mites; nematodes; unicellular hairs of *Barteria fistulosa;* dirt; and numerous spores of many different types (Pl. XLIV, fig. 1; Pl. XLV, fig. 4). Occasionally, they contain bits of extraneous plant tissues, pollen, fragments of malaxated insects, etc.

Pellets dissected from the heads of imagines contain a similar assortment of substances, but usually in somewhat different proportions. In other words, they have a smaller admixture of animal tissue. This is due, in all probability, to the fact that the worker nurses add fragments of coccids to their pellets before feeding them to the larvæ.

Although the larvæ undoubtedly feed upon the fragments of coccids, it is difficult to determine how much of the miscellaneous material is actually eaten by them. The larval stomach contains a structureless mush, so that analyses of the contents of this organ are of little significance in this connection. There is a similar difficulty in distinguishing

between detritus and food residues in the infrabuccal chambers of the imagines. The fragments of malaxated insects are food residues, but the aërial hyphæ and fragments of medullary tissue may be vegetable débris, which adhered to the surfaces of the imagines during the process of cleaning and enlarging the domatia.

Pellets of *Crematogasters*

The infrabuccal sacs of the *Crematogasters* which inhabit the *Cuvieræ* and *Plectronia Laurentii* also contain substances both from within and without the domatia. Although many of the pellets have an admixture of malaxated insects, they do not contain fragments of the coccids which inhabit the myrmecophytes. Not infrequently, the pellets are composed entirely of bits of the ambrosia-like mycelia, or fragments of parenchyma which are packed with this fungus. Most of the pellets, as in the case of *Pachysima*, contain malaxated medullary tissue, and dirt, pollen, hairs, spores, and other extraneous substances.

The infrabuccal sacs of the *Crematogasters* which inhabit the *Barteriæ* and *Sarcocephalus* are more or less completely filled with the same general assortment of substances which occur in the infrabuccal pellets of *Crematogaster africana* subspecies *laurenti* variety *zeta* and *C. impressiceps* variety *frontalis*; except that the bits of ambrosia-like mycelia are replaced by fragments of chromogenic, aërial hyphæ which grow within the ant-inhabited cavities of these myrmecophytes.

Nutritive Significance of the Callus-heteroplasias

The problem of determining the exact nutritional significance of the callus-heteroplasias in the *Cuvieræ, Plectroniæ, Barteriæ*, and *Sarcocephalus* is complicated by the presence of coccids which feed upon these tissues. In other words, the question arises as to whether these structures are induced by the ants primarily for their own consumption or for feeding the coccids. Histological evidence indicates that the nutritive layer is gnawed and rasped by the ants, and fragments of this tissue occur in the pellets of the *Crematogasters*, but these facts in themselves do not afford a solution of the difficulty. Nor does the absence of 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 Coccidæ.

Relations Between Ants and Coccids

The well known aphid- and coccid-tending habits of the Cremato-gastrini suggest that the coccids are introduced into the myrmeco-phytes by the *Crematogasters* and carefully tended by them as "milch cows." That the *Crematogasters* actually devote considerable attention to the coccids is indicated by the following observation of Kohl (1909):

Nicht selten fand ich Cocciden-Kolonien auch ausserhalb der Höhlungen, so auf *Plectronia Laurentii*, wo sie sich in einem Gehäuse befinden, das von den Ameisen aus fein zerkleinerten pflanzlichen Bestandteilen hergestellt wird, nachdem letztere mittels einer von ihnen ausgeschiedenen klebrigen Flüssigkeit verkittet wurden. Diese Schildläusekammern standen vielfach mit den innern Nisträumen durch eine oder mehrere Öffnungen in Verbindung.

It seems probable, however, that the large colonies of coccids in *Barteria fistulosa* may be purely adventitious. The Pseudomyrminæ are not known to tend Aphididæ, Coccidæ, Membracidæ, Fulgoridæ, or Psyllidæ, and, as I have indicated on preceding pages, the *Pachysima* imagines actually carve up the coccids and feed them to their larvæ.

Nutritive Value of Medullary Tissue

The ants scarify the walls of the myrmecodomatia of the *Cuvieræ*, *Barteriæ*, *Plectroniæ* and *Sarcocephalus*, excavating the remains of the succulent, inner portions of the pith and removing more or less of the thick-walled medullary tissue. Although fragments of these tissues occur abundantly in the infrabuccal pellets of the imagines, there is, unfortu-nately, no conclusive evidence to indicate whether the ants actually feed upon them, or remove them merely for the purpose of cleaning and en-larging the domatia; in other words, whether the fragments in the infra-buccal sacs are food residues or detritus.

Nutritive Value of Fungi

All of the ant-inhabited plants (species of *Acacia*, *Triplaris*, *Cecro-pia*, *Nauclea*, *Enterolobium*, *Myrmecodia*, and *Hydnophytum*, as well as *Cuviera*, *Vitex*, *Plectronia*, *Barteria*, and *Sarcocephalus*) of which I have succeeded in obtaining suitable material have a more or less luxuriant growth of fungi upon the inner walls of their myrmecodomatia. These fungi are cropped by the ants and fragments of them are taken into the infrabuccal cavities of the imagines. However, as I have shown elsewhere (Bailey, 1920), there is no reliable evidence to indicate that these fungi are cultivated and fed upon by the ants, and are not purely adventitious and merely cropped in order to prevent them from obstructing the domatia and interfering with the broods.

Ants and Nematodes

I have shown that the infrabuccal pellets of *Pachysima* and the accumulations of detritus of *Crematogaster impressiceps* variety *frontalis* contain numerous nematodes (Pl. XXXVIII, fig. 3). Janet (1893) has pointed out that certain nematodes pass their larval stages in the pharyngeal glands of *Formica rufa* Linnæus, *Lasius flavus* (Fabricius), etc., and that sexed individuals occur in the detritus of the ant colonies. In the case of *Pachysima æthiops*, the nematodes evidently work their way into the infrabuccal sac and subsequently are transferred to the larval trophothylaces or are cast out in voided pellets.

Amber-colored Substance

I have called attention to the peculiar amber-colored substance in the normal and abnormal tissues of the *Cuvieræ*, *Barteriæ*, and certain of the *Plectroniæ*, which serves not only as an excellent "culture-medium" for fungi, but is fed upon by coccids and ants. When seen *en masse*, it is dark-colored and opaque, but in freshly-cut, thin, microscopic preparations is a translucent or hyaline, bright-golden-yellow, amorphous substance. It gradually darkens, if sections are left in alcohol or water, turning a reddish brown. The substance shrinks in drying and swells very considerably when remoistened with alcohol or water, but is insoluble in these liquids and also in ether, chloroform, benzol, carbon bisulphide, acetic, hydrochloric, and sulphuric acids, and cuprammonia. It dissolves readily, however, in dilute solutions of caustic soda, caustic potash, and nitric acid. It does not give a red color-reaction in Sudan III, alcanna, corallin, or hot or cold phloroglucin and hydrochloric acid, but takes on a reddish tinge in Hanstein's aniline and in hydrochloric acid. It turns dark in iron salts and stains readily in aniline-blue. In iodine and cold Millon's reagent, it takes on a dirty greenish color, but, when heated in the latter reagent, turns a dark brick-red. It retains its original color in hot concentrated nitric acid, but turns a darker yellow or orange brown on moistening with strong ammonia.[1]

I suspect that the substance is a complex mixture, containing proteins and carbohydrates but, in the absence of abundant material and an extensive chemical investigation, I have not been able to secure any reliable clue in regard to its composition.

Of course, it should be kept in mind that the material which I have studied consists entirely of dried specimens and of myrmecodomatia

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[1]When the substance has turned dark reddish brown, by standing in water or alcohol or by drying in air, the original bright-golden-yellow color is restored by treatment with nitric acid.

preserved in 70%–90% alcohol. Therefore, the substance in question may have been considerably modified (by phenomena of coagulation, oxidation, etc.) and may have existed in a more fluid phase in living plants. If it has not undergone solidification, the coccids must secrete substances which act upon it in order to render it sufficiently fluid to pass through their sucking mouth-parts.

Similar amber-colored substances occur in a number of other myrmecophytes, particularly in rubiaceous plants. The cells of the peripheral layer of medullary tissue in the myrmecodomatia of certain *Cecropiæ* are filled with a translucent amorphous material[1] whose microchemical reactions parallel those that have been outlined above.

The exact role which these substances play in the nutrition of ants, and of the coccids and fungi which are frequently associated with them, deserves to be carefully investigated.

Theories of Myrmecophily and Myrmecophytism
Hypothesis of Richard Spruce

During the last sixty years there has been considerable speculation concerning the significance of myrmecophytism. In his explorations of the Amazonian and Andean regions of South America (1849–1864) Richard Spruce encountered many plants having peculiar structural modifications, foliar sacs, hollow fistulose stems, etc., which were occupied by ants. Upon returning to England, Spruce prepared a paper[2] in which he endeavored to account for the origin of these remarkable myrmecophytes. This paper was read before the Linnæan Society on April 15, 1869, but unfortunately did not appear in print until 1908, owing to the fact that the Council of the Society would not authorize its publication unless Spruce made certain fundamental changes in the text. This Spruce refused to do.

The kernel of Spruce's hypothesis is contained in the following paragraph:

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.

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[1]Fiebrig's (1909) conclusion that the reddish brown color is produced by oxidations induced by formic acid is not likely to be substantiated.

[2]"Ant-agency in plant-structure; or the modifications in the structure of plants which have been caused by ants by whose long-continued agency they have acquired sufficient permanence to be employed as botanical characters."

He supposed that the ants induced the formation of the abnormalities in order to provide themselves with domatia during periods of inundation, and drew largely upon his remarkable fund of information concerning the flora of tropical America in support of this idea. He pointed out that the majority of the myrmecophytes occur in low swampy regions or regions that are periodically inundated, and emphasized the fact that species which are entirely submerged during periods of high water are normal, whereas species which are only partly covered tend to be myrmecophytic.

Seeing, then, how the sacs on the leaves have originated, and what purpose they serve, it is plain that a species of *Tococa*, like *T. planifolia*, inhabiting the very river's brink, and liable to be completely submerged for several months of every year, could never serve as a permanent residence for ants, nor consequently have any character impressed on it by their merely temporary sojourn; even if their instinct did not teach them to avoid it altogether, as they actually seem to do; whereas the species of *Tococa* growing far enough inland to maintain their heads above water even at the height of flood are thereby fitted to be permanently inhabited, and are consequently *never destitute of saccate* leaves, nor at any season of the year clear of ants. Nearly all tree-dwelling ants, although in the dry season they may descend to the ground and make their summer-houses there, retain the sacs and tubes above-mentioned as permanent habitations; and some kinds of ants appear never to reside elsewhere, at any time of year. There are some ants which apparently must always live aloft; and the *Tococa* dwellers continue to inhabit Tococas where there is never any risk of flood, as in the case of *T. pterocalyx*, which grows on wooded ridges of the Andes. Their case is parallel to that of the lake-dwellers of the mouth of the Orinoco and the inundated savannas of Guayaquil, whose descendants must needs elevate their houses on stages six feet or more in height, although nowadays erected on rising ground far beyond the reach of floods or ocean-tides (Spruce).

Spruce did not consider that there was any true symbiosis between the ants and the plants as 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.

Belt's Theory of Symbiosis

In 1874 Belt published the results of his observations upon leaf-cutting ants and certain. myrmecophytic *Acaciæ*, and formulated an ingenious theory of myrmecophily. He concluded that the ants which inhabit the "bull's-horn" *Acaciæ*.

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. For these services the ants are not only securely housed by the plant, but are provided with a bountiful supply of food; and

to secure their attendance at the right time and place this food is so arranged and distributed as to effect that object with wonderful perfection. The leaves are bi-pinnate. 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. Of this the ants are very fond; and they are constantly running about from one gland to another to sip up the honey as it is secreted. But this is not all; there is a still more wonderful provision of more solid food. 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 the microscope, this little appendage looks like a golden pear. When the leaf first unfolds, the little pears are not quite ripe and the ants are continually going from one to another, examining them. When an ant finds one sufficiently advanced, it bites the small point of attachment; then, bending down the fruit-like body, it breaks it off and bears it away in triumph to the nest. All the fruit-like bodies do not ripen at once, but successively, so that the ants are kept about the young leaf for some time after it unfolds. Thus the young leaf is always guarded by the ants; and no caterpillar or larger animal could attempt to injure them without being attacked by the little warriors.

These facts lead Belt to the conclusion that the function of the honey-secreting glands of plants is to attract insects which protect the flower-buds and leaves from the attacks of phytophagous insects and herbivorous mammals; and, by analogy, that the sugary secretions of various plant lice, scale insects, and leaf-hoppers have a similar function in attracting ants for the protection of these insects.

Delpino's Hypothesis

A similar explanation of the function of extrafloral nectaries was put forward by Delpino in a paper read in 1873 (published in 1874–75).

What then is the function of the extranuptial nectaries, which are found on the caulinary leaves, on the bracts, and on the calyx? Though I reserve for another paper the publication of my studies of such and other extra-dichogamic relations between plants and insects, I do not hesitate to announce now that the chief function of these nectaries is to place the ants, wasps, and *Polistes* in the position of sentries and guards, to prevent the tender parts of the plant from being destroyed by larvæ.[1]

He elaborated this hypothesis in subsequent papers and reached the following conclusion (1889) in regard to myrmecophilous plants:

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[1] "Qual è dunque la funzione dei nettarii estranuziali, sia che si trovino sulle foglie cauline, sulle brattee o sul calice? Quantumque noi ci riserbiamo in altro lavoro di publicare i nostri studii sovra siffatte ed altre relazioni estradicogamiche tra le piante e gl'insetti, non esitiamo fin d'ora ad enunciare che riffatti nettarii hanno per funzione principale di costituire nelle formiche, nelle vespe, nei *Polistes* altrettante vigili sentinelle e guardiani per impedire che le parti tenere delle piante siano divorate dai bruchi."

Kerner von Marilaun (1876) has also advanced the view that the function of extrafloral nectaries is to prevent ants from plundering the nectar from flowers and thus interfering with the normal processes of insect-fertilization.

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.[1]

Beccari's Hypothesis

Beccari (1884–86), like Richard Spruce, endeavored to account for the origin of the peculiar structural modifications of various myrmecophytes upon the basis of the Inheritance of Acquired Characters. The following extracts from his beautifully illustrated work upon the myrmecophytes of Malasia are significant in this connection:

Among insects, *e. g.* the ants, endowed with burrowing habits and also attracted by nutritive substances and fleshy tissues, may have sought, by piercing the bark and the ligneous parts, to enter certain branches or certain twigs. Having taken away the easily removable tissues, they may have succeeded in obtaining a commodious cavity in which to nest. During this performance the ants may have stimulated, although unconsciously, the walls of the inhabited cavity, which in consequence of the stimulus, may have grown and become ulteriorly modified. So that finally, in the course of time, they may have produced twigs that were normally provided with sheltering cavities. The argument, if valid for the twigs, may also be applied to the spines, to the pouches on leaves or roots, or to any other organ. If the ants did not always use a definite spot in order to gain access into the cavity, or if the entrance was made on a place where no sensitive protoplasma was present, the aperture would not become hereditary (*Acacia cornigera, Endospermum*); if, on the contrary, the ants continually selected some particular spot for perforation, and especially if the latter was near accumulations of sugary or mucilaginous substances, areoles may be produced where the tissues offered less resistance than elsewhere (*Cecropia*) and which subsequently became absolutely open (*Clerodendron fistulosum*). . . . The "food-bodies" of *Acacia cornigera* seem to me to have perhaps had this origin. . . . I am therefore of opinion that, because of the long time during which the stimulus of the ants acted upon the bulbose hypocotyle of *Myrmecodia* and related genera, a period of hereditary production (perhaps more pronounced in certain species than in others) has begun even of the galleries of the tuber, which are the essential part of the organ with which the plant acts as a host. In this way it may happen that this organ at once assumes the growth of a tuber, which, under certain circumstances, may remain in life and also grow independent of ants.[2]

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[1] "Nel caso delle specie mirmecofile, la piante lavora per la formica in due modi o somministrandole un alimento zuccherino, o fornendole comodità di alloggio, e la formica lavora per la piante difendendola dai suoi nemici."

[2] "Le formiche per es. fra gli insetti, dotate di abitudini perforatrici, attratte forse da sostanze nutritizie o da tessuto flosio, possono aver cercato, perforando la scorza e la parte legnosa, di introdursi nell' interno di certi rami o di certi fusti, e quivi asportando il tessuto facilmente removibile, possono esser riuscite a procurarsi una cavità comoda, nella quale fare il nido. In queste manovre le formiche avranno stimolato, anche senza volerlo, le pareti della cavità abitata, la quale in causa 'degli stimoli ricevuti potrà accrescersi e modificarsi a seconda delle circostanze, per finire coll' andar del tempo a dare origine per eredità a dei fusti, che naturalmente producono cavità ospitatrici. Il ragionamento che vale per i fusti, può egualmente applicarsi alle spine, ai piccioli delle foglie a alle radici od a qualunque altro organo. Se le formiche non si saranno sempre servite di un posto determinato per accedere nella cavità, o se l'apertura sarà stata praticata in luogo dove non esiste protoplasma sensibile, l'apertura non si renderà ereditaria (*Acacia cornigera, Endospermum*); se però le formiche approfitteranno costantemente di qualche punto speciale per la perforazione e sopratutto se questo sarà un luogo dove esistono accumulamente di sostanze zuccherine o mucillaginose, si potranno produrre delle areole, dove il tessuto offrirà meno resistenza che altrove (*Cecropia*) a che alla lunga diventerà assolutamente pervio (*Clerodendron fistulosum*). . . . I "food-bodies" dell' *Acacia cornigera*, mi pare che potrebbero avere avuto questa origine. . . . Sono però d'opinione che in causa del lungo tempo durante il quale lo stimolo delle formiche agisce sugli ipocotili imbulbiti delle *Myrmecodia* e generi affini, sia incominciato (forse in talune specie più che in altre) un periodo di produzione ereditaria anche per le gallerie del tubero, che costituiscono la parte essenziale dell' organo ospitatore, per cui può accadere che una volta avviata la vegetazione dei tuberi, questi in certe circostanze possano mantenersi in vita ed anche accrescersi indipendentemente dalle formiche."

Other Hypotheses

Fritz Müller (1880–81) and A. F. W. Schimper (1888) brought together considerable evidence, particularly in the case of *Cecropia*, to show that myrmecophytism is a true symbiosis, that the ants actually protect their hosts and that the food-bodies, extrafloral nectaries and many of the peculiar structural modifications of myrmecophytes are adaptations for the purpose of attracting ants. It should be noted in passing, however, that "Schimper's theory" of myrmecophily is not essentially different from the earlier hypothesis of Belt.

In 1900 Buscalioni and Huber published a short paper, "Eine neue Theorie der Ameisenpflanzen," in which they noted the abundance of myrmecophytic plants in swampy or inundated regions, and suggested that myrmecophytism originated under environmental conditions of this character, a view which, as I have shown, was championed by Spruce.

It is evident, accordingly, that there are in reality but two distinct theories of myrmecophytism; the Belt-Delpino hypothesis, or theory of symbiosis (myrmecophily), and the Lamarckian theory of Richard Spruce. The "theories" of Fritz Müller, Beccari, Schimper, Buscalioni and Huber, and others resemble in their fundamental features one or the other of these hypotheses.

Critics of the Theory of Myrmecophily

The Belt-Delpino hypothesis and the adherents of myrmecophily have been severely criticised in recent years by a number of different investigators. Möller (1893), Ule (1900), Rettig (1904), H. von Ihering (1907), Madame Nieuwenhuis von Üxküll-Güldenbrandt (1907), Fiebrig (1909), Wheeler (1913), and others have assailed the principal bastions of this theory and have succeeded in demolishing many of the principal arguments advanced in its support. Thus, it has been demonstrated that the ants are not sufficiently effective guardians of the plants to account for the origin of the various structural modifications of myrmecophytes through the action of Natural Selection. This is true even in the classical cases of the myrmecophytic *Cecropiæ* and *Acaciæ*. Furthermore, many plants which are not inhabited or frequently visited by ants are provided with pseudo-domatia, prostomata, food-bodies, extrafloral nectaries, etc.

Present Status of the Problem of Myrmecophytism

Although these investigators have succeeded in overthrowing the ingenious theory of Belt-Delpino and in showing that myrmecophytism is, in all probability, not a phenomenon of true symbiosis, but rather one

of parasitism, they have failed to provide a satisfactory working hypothesis to account for the origin and functional significance of the various inherited structural peculiarities of myrmecophytes. For example, Madame Nieuwenhuis von Üxküll-Güldenbrandt (1907) states, at the end of her comprehensive monograph upon extrafloral nectaries, that biologists have no more idea in regard to the true meaning, origin, and functional significance of these glandular structures than they did in the time of Linnæus. We are equally in the dark concerning the so-called Beltian and Müllerian food-bodies, saccate leaves, fistulose or swollen, hollow stems and branches, prostomata, etc. It is true that the work of Treub (1883, 1888), Rettig (1904), Miehe (1911), and others indicates that the pseudobulbs, galleries, and papillæ of the *Myrmecodiæ* have a physiological origin and function, but their results are not entirely conclusive.

In view of the taboo that has been placed upon the Inheritance of Acquired Characters (owing to the seeming impossibility of proving, or disproving, the validity of this phenomenon) the simple Lamarckian explanations of Richard Spruce and Beccari are not likely to find many ardent supporters. Furthermore, the frequent occurrence of the same peculiar structural modifications, in plants which are not inhabited or visited by ants, is as serious a stumbling block in the way of the Spruce-Beccari hypothesis as it is in that of Belt-Delpino.

The present status of the problem of myrmecophytism may be summarized, therefore, 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 pseudo-domatia, 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.

My own observations upon myrmecophytism among African plants lead me to believe that the relationship is solely one of parasitism; but one in which the behavior of the parasitic insects is particularly significant. Although there appears to be no valid reason for supposing that the ants have been, or are now, concerned in the origin and development of the pseudo-domatia or peculiar modifications of the central cylinder that are associated with phyllotaxy, histological and other evidence indicates conclusively that the callus-heteroplasias, as well as the remarkable exit apertures of *Vitex Staudtii*, are traumatisms induced by the ants.

Origin of the Pseudo-gall-forming Habit

It is to be emphasized that the pit-like excavations, containing nutritive callus-heteroplasias, occur in plants of different growth forms (belonging to three distinct orders, Parietales, Tubifloræ, and Rubiales) and are produced, not only by the "obligatory" *Viticicola* and *Pachysimæ*, but also by the ubiquitous, "facultative" *Crematogasters*. In the case of the highly modified and specialized *Viticicola tessmanni*, the gall-like structures of *Vitex Staudtii* are very complex histologically and their production appears to be under more delicate control, as is evidenced by their characteristic form and structure and very symmetrical distribution. In the flacourtiaceous and rubiaceous myrmecophytes, on the other hand, not only do the individual excavations vary greatly in size and shape, but their distribution is more or less erratic and there are numerous evidences of "trial and error" in their production. Whereas in *Vitex Staudtii* the ants almost invariably cut their excavations to just the right depth (the level of the cambium and inner cortex) to produce ingrowths of delicate, undifferentiated, nutritious parenchyma and gnaw away the inner margin of this layer at a rate which yields the most favorable results, the *Crematogasters*, *Engrammata*, and "obligatory" *Pachysimæ* frequently cut their way to the outer cortex, epidermis, or exterior and induce the formation of heteroplasias which, owing to the differentiation of more or less sclerenchyma, wound-wood, wound-cork, etc., are less nutritious and more difficult to control during the subsequent process of feeding.

The question naturally suggests itself, how did these pseudo-gall-forming habits originate among ants? There are certain general tendencies in the growth of plants and in the activities of ants which appear to throw some light upon this problem.

In woody plants, the cortex and cambium (and its derivative tissues) are under a certain equilibrium as regards mechanical strains and stresses, osmotic forces, distribution of moisture and food-substances, etc. When this equilibrium is disturbed by mechanical injuries, the polarity, rate of division, physiological activity and differentiation of the cells of the cambium and cortical parenchyma are more or less profoundly modified, depending upon the type and severity of the injury, the kind of plant, and its stage of development, etc. Abrasions and perforations, which extend through the cortex, phloem, and cambium to the xylem or medulla, tend to alter the polarity of the cambial cells in the immediate vicinity of the injury and to cause them to divide more actively. This change in polarity and acceleration in growth, which commonly extends to the

parenchyma of the overlying tissues, produces lateral out-growths of delicate, thin-walled, unlignified, more or less isodiametric cells from the sides of the wound. These callus-formations gradually bridge over the gap in the side of the stem and lead ultimately to a regeneration of the missing portions of the cambium, cortex, xylem, and phloem. However, the differentiation of the cells of the callus does not result at once in the production of normal tissues, but of so-called wound-wood, wound-cork, etc. These wound-tissues vary greatly in form, structure, and arrangement, depending upon a number of different factors. Furthermore, there tends to be a considerable concentration of food-substances (protein, fats, sugars, etc.) in callus-heteroplasias and frequently of gums, mucilages, resins, tannins, etc. in the tissues which are differentiated from them.

The entrance and exit apertures, made by ants in the sides of myrmecodomatia, usually become occluded by wound-tissues unless they are kept open by the ants. For example, F. Müller (1880–81) found that in *Cecropia* the perforations made by *Azteca* queens in entering the primordial, internodal chambers frequently heal over and have to be reopened upon the exit of the young colony. Similar occluded apertures are of common occurrence in abandoned myrmecodomatia and domatia whose inhabitants have died or been killed by other insects. In clearing the entrance and exit holes, the ants are forced to gnaw upon the callus-heteroplasias. Therefore, since these tissues are usually well supplied with nutrient substances, as is indicated not only by microchemical analyses, but also by the fact that they are frequently fed upon by coccids, it might be expected *a priori* that the ants would discover the nutritive value of the callus and in many cases endeavor to increase its volume. The simplest and most direct method of producing additional callus-heteroplasias in the African myrmecophytes, and in other plants having similar myrmecodomatia, is for the ants to cut through to the cambium from the inside of their domatia. The moist, dark environment in the interior of the domatia favors a luxuriant growth of callus and tends to retard the differentiation of its cells, whereas the general environment upon the exterior of the myrmecodomatia appears in most cases to have an opposite effect. This is indicated by the structure, form, and development of callus-outgrowths from perforations in the walls of fistulose stems and branches. The heteroplasias tend to grow more rapidly in the direction of the moist central chambers than they do laterally or towards the exterior, so that they frequently project more or less into the domatia; and, as shown in Pl. XL, fig. 1, the differentia-

tion of the cells proceeds more rapidly in the external than in the inner portions of the heteroplasias.[1]

In the myrmecophytic *Cuvieræ*, *Plectroniæ*, and *Barteriæ*, the callus heteroplasias which grow out from the margins of the entrance apertures resemble those that develop in the pit-like excavations. When the cells of the latter are filled with an amber-colored substance, the elements of the former contain this material which is fed upon by coccids and also apparently by 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 facultative *Crematogasters* as well as the obligatory *Pachysimæ* and *Viticicola*. The remarkable fact is that the pseudo-cecidia should occur in a number of African myrmecophytes, belonging to three distinct orders, and not have been recorded in similar myrmecophytes from other tropical or subtropical regions. Of course, this may be due largely to structural and other differences in the myrmecodomatia, or to differences in the general growth-conditions of the vegetation, but I am inclined to believe that the phenomenon occurs in extra-African myrmecophytes and has been overlooked. For example, I find that the myrmecodomatia of *Nauclea formicaria* Elmer and of an unidentified Philippine myrmecophyte contain bisymmetrically arranged lateral excavations and callus-heteroplasias which resemble those of the African *Cuvieræ*. These myrmecodomatia were inhabited by species of *Decacrema* and *Camponotus* respectively. Furthermore, as has been pointed out earlier in this paper, the "stomatomes" of *Cecropia*, which contain colonies of *Aztecæ*, resemble the heteroplasias of *Plectronia* species *A*, and, although they are not situated in pit-like excavations, may prove to be homologous structures.

Sclerenchymatous Rings and Caps of *Vitex Staudtii*

Just as certain abnormal environmental conditions, caused by mechanical injuries, lead to the formation of delicate, undifferentiated callus, others produce the transformation of thin-walled parenchyma into sclerenchyma. Thus, one commonly finds more or less sclerenchyma in those portions of the bark which overlie the excavations in the walls of the myrmecodomatia of the *Cuvieræ* and *Plectroniæ*. Similarly, the outer surfaces of the exit apertures are often more or less completely jacketed by sclerenchyma. When the inwardly projecting callus has

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[1]In *Cecropia* these ingrowths of callus, which are unusually large and conspicuous, may continue to grow and even proliferate after the entrance apertures are entirely closed by wound-tissue.

been completely gnawed away by the ants, as frequently happens, this dense layer of tissue must serve as a more or less effective barrier to the growth of additional occluding tissue from the sides of the apertures.

I have emphasized the fact that in *Vitex Staudtii* the lateral excavations and callus-heteroplasias are remarkably similar in form and structure and very symmetrically distributed. There is an equal uniformity in the production of sclerenchyma, as is evidenced by the peculiar sclerenchymatous caps and rings which are such characteristic features in the anatomy of this myrmecophyte. In the absence of necessary experimental investigations, it is not possible to determine, however, whether *Vitex Staudtii* possesses a more pronounced tendency towards the formation of sclerenchyma than other myrmecophytes or whether the production of these peculiar structures is due solely to a more delicate control of ordinary traumatic phenomena by the highly specialized *Viticicola lessmanni*.

In conclusion, it is to be emphasized that these tropical "biocœnoses," in which representatives of the higher plants, fungi, ants, coccids, and nematodes are intimately associated, deserve to be carefully and critically studied in the field. They should form the basis for some exceedingly interesting physiological and ecological investigations.

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