Sporidia scarcely perfect, but apparently much smaller than in C. æruginosum. The matrix is not discoloured.

- 435. CENANGIUM BRASILIENSE, Mont. Ann. des Sci. Nat. sér. 4, v. 371.
- On bark. Goyaz (Wedd.).

436. РНАСІЛІИМ DENTATUM, Kunze, Berk. in Hook. Journ. (1851) 17. Caripi (Spruce).

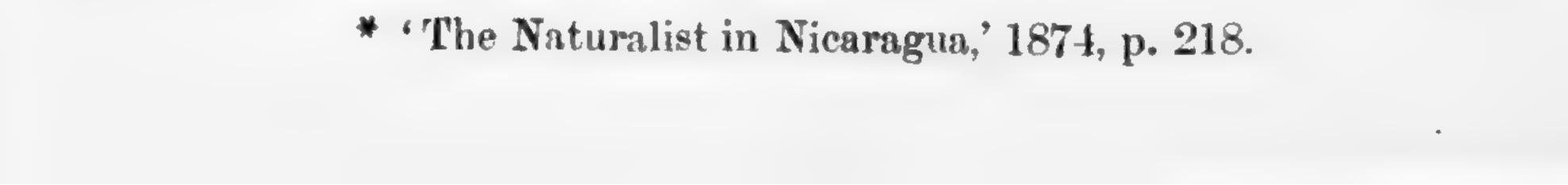
- 437. RHIZOMORPHA CORYNEPHORA, Kunze in Weig. Exs.; Berk. in Hook. Journ. (1856) 277.
- S. Antonio de bon vista, Rio Javary (Traill, no. 173). Panuré (Spruce, no. 149). Traill's no. 22 is also a Rhizomorpha.

On the Glandular Bodies on Acacia spharocephala and Cecropia peltata serving as food for Ants. With an Appendix on the Nectar-glands of the common Brake Fern, Pteris Aquilina. By FRANCIS DARWIN, M.B., F.L.S.

[Read June 1, 1876.]

(PLATE VI.)

THESE structures were discovered by Mr. Belt; and the part which they play in the economy of the plant is described in his delightful book\*, from which the following description is taken. Fig. 1 (Pl.VI.) represents a small branch of Acacia sphærocephala; at the base of the petiole is seen a pair of sharp curved spines, h h, from which the tree receives its name of the Bull's-horn Thorn. These spines are hollow and are inhabited by ants; and at certain seasons hundreds of the colonists may be seen running about over the young leaves, passing in and out of their nest through an aperture made at the base of the spine. The ants form a standing army for the tree, and not only prevent cattle &c. browsing on it, but also protect it from the ravages of the leaf-cutting ants. So serious is the latter danger, that the tree is actually unable to exist without its guard of colonists. To ensure the presence of ants about the young leaves two attractions are offered by the Acacia :---first the nectar secreted by a crater-formed gland situated at the base of the petiole, and shown at g g in fig. 1;



secondly, a little golden pear-shaped body developed at the extremities of some of the leaflets of the bipinnate leaf. In the enlarged drawing, fig. 2, the general aspect of the pear-shaped bodies is seen. I have ventured to rename these structures (the rations served out to the standing army of ants) *food-bodies*, including under this term the analogous structures in *Cecropia* immediately to be described.

A few months ago my father received a letter from Herr Fritz Müller, the well-known naturalist, residing at St. Catharina, in Brazil; this letter was published in 'Nature,' Feb. 17, 1876, p. 304. Fritz Müller shows that the ants inhabiting the hollow stems of a Cecropia mentioned by Mr. Belt are supplied with food-bodies analogous to those of the Acacia. Here the food-bodies are not developed on the tips of the leaflets, but at the base of the petiole of the leaf, on its underside, emerging, as Fritz Müller says, like asparagus from a bed, out of the cushion of hairs which clothe the pulvinus. The sweet liquid for the ants is not supplied by glands, but by the scale-insects kept by the ants in the hollow stem which forms the nest of the colony. Thus we have in Cecropia the same maryellous protection as in Acacia; moreover I hope to be able to show that not only are the food-bodies of these widely distinct plants histologically identical, but that they are actually homologous one with the other-though one is an appendage to the leaves, the other a growth from the pulvinus. Herr Fritz Müller had informed my father that he intended to publish an account of the Cecropia; and through the courtesy of Dr. Hermann Müller and his son, I was enabled to see a copy in extenso of Fritz Müller's forthcoming paper. As he does not enter into the minute structure of the food-bodies, it seemed worth while to attempt its investigation; this I have been fortunate enough to be able to do through the kindness of Dr. Hooker, who has placed living plants of both the Acacia and the Cecropia at my disposal. I have worked chiefly at the food-bodies of Acacia, as being easier to manipulate, and also because I learn from Dr. H. Müller that Prof. Strasburger, of Jena, will probably describe those of Cecropia.

ACACIA SPHÆROCEPHALA.—The leaf is bipinnate and about 9 or 10 centims. in length; it springs from the base of the gigantic pair of thorns and beens a minute spine at its upper ord. The

pair of thorns, and bears a minute spine at its upper end. The	
food-bodies are developed on the six or seven lower pairs of leaf	
a source are developed on one six of seven tower pairs of lear	

lets; they are about 2 millims. in length, and are shaped like a pear with one side much flattened. Longitudinal sections examined with a low power show that the food-body is made up of cellular tissue continuous with that of the leaf and included within the epidermis. The cells are somewhat elongated, those at the base giving in section a fairly rectangular outline ( $064 \times 016$ millim.); in transverse sections the cells appear nearly circular in outline. A fibro-vascular bundle, continuous with the midrib of the leaf, runs for a considerable distance into the food-bodies, e. g. for  $\cdot 6$  or  $\cdot 77$  of their length, and terminates blindly in a few short bifurcations of the spiral vessel. Methods employed.-Hardly any thing need be said on this head; the food-bodies are of such a consistence as to allow of sections being cut in the usual way. I have found it convenient to colour the embedding material pink with alkanet, for the sake The of the contrast of colour with the pale yellow food-body. various reagents used will be detailed in the sequel. Minute structure.—Examined with a high power, the cells are found to contain a granular protoplasmic body, in which strongly refracting oil-globules are embedded. There is a spherical nucleus 0064 millim. in diameter, staining brightly in carmine, aniline, &c. In some preparations the protoplasm lies free in the cellcavity; in others it fills it entirely. It is of a firm texture, and may often be seen floating out in a mass from a ruptured cell. It exhibits the following reactions characteristic of protoplasm :---1. It takes a deep yellow colour with iodine.

2. It assumes a fine rose tint on being placed in strong sulphuric acid after having been soaked in syrup.

3. Strong nitric acid and subsequent treatment with a solution of caustic potash give the yellow colour of xanthoprotein.

The metaplasmic particles which give it a granular appearance are removed by potash or acetic acid; under this treatment the protoplasm clears up, and the oil is well shown ; fig. 3 represents a section in this condition.

The oil, which is seen to consist of globules of various sizes, gives the following reactions :---

1. It is soluble in ether, absolute alcohol, and in a mixture of turpentine and creasote, and is not soluble in water or glycerine.

2. It is coloured green by strong sulphuric acid\*.

\* This test has been applied to oils by Heydenreich and Penot, see Dict. of

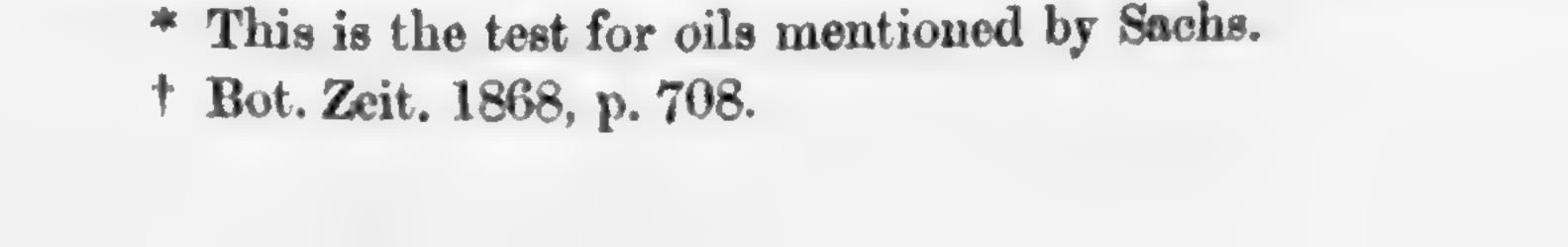


3. Tincture of alkanet stains it bright pink\*. It is not coloured by other staining fluids.

The green colour with sulphuric acid is the only one of the above reactions which would show that the globules are oil and not resin; for Hanstein + mentions alkanet as staining resin; but the fact that the ants search greedily after the food-bodies seems to show that they are oleaginous.

Relation between the Oil and the Protoplasm.—Sections cleared with caustic potash show plainly that the oil is embedded as separate drops in the protoplasm; and similar sections from which the oil has been dissolved with ether &c. exhibit the cavities in which the oil is thus contained. The matrix may be stained with alkanet; and one then sees the crimson protoplasm pierced in all directions by smooth-walled cavities corresponding with the oil globules seen in the potash specimens, fig. 3. Sections stained rather less brightly and from which the oil has not been removed, show a pretty contrast between the bright crimson oil drops and the less brilliant matrix. Where the oil is in the form of a number of very minute drops of equal size, the protoplasmic matrix (as seen in thin sections cleared with potash and with creasote) exhibits a delicate network, as shown in fig. 4.

It may be of interest to note that the food-bodies of Acacia partially resemble in structure some other forms of nutrimentstores in the vegetable kingdom. It appears that the crater glands and the food-bodies together supply nutriment sufficient to support the ants; it is therefore evident that the latter must be considered in the light of protein stores as well as of stores of carbohydrates. We may compare them analogically with the endosperm of seeds, in which these substances are also stored. Now in some seeds the oil is found as drops in the cavities of a protoplasmic matrix, just as in the food-bodies; possibly also the (proteinaceous?) granules in the protoplasm of the food-bodies may be compared to aleurone grains. Homologies and Development.-In the adult state the upper leaflets terminate in minute points, '1 millim. in length. They appear to be embryonic structures ; for they are relatively well developed in a very early stage of growth, and as the leaf grows they remain stationary and shrivel away. If we examine an extremely young leaf, we find that all the leaflets, both upper and lower, termi-



nate in constricted points composed of cells differing slightly in appearance from those of the rest of the leaflet; now, although the points on the lower leaflets which are destined to become food-bodies soon outgrow those on the upper ones, yet there can be no doubt that they are morphologically identical with one another. Foodbodies are usually developed on the six or seven lower pairs of leaflets; but sometimes, by an arrest of development, one of these terminates in a simple point hardly larger than those on the upper leaflets. This is seen in fig. 2, where p ought normally to have grown into a body like  $f^3$ . In accordance with the principle of compensation of growth, the leaf is frequently dwarfed in correspondence with the development of the food-bodies, as for instance at  $f^1$  in fig. 2; occasionally the leaf proper is quite aborted, and the food-body is attached to the petiole simply by a minute stalk. The question next arises, With what structures in other plants are these points homologous? If we imagine the bipinnate leaf of the Acacia converted into a pinnate leaf by the coalescence of the pinnæ, the tips of the old pinnæ will become the teeth of the new serrated pinnæ. Now, withered tips are found on the points of the serrations of many leaves; and Reinke has shown that such points are the remains of glands which are highly developed at a very young stage of growth, and die off as the leaf grows\*. I conclude therefore that the food-bodies are homologous with the serration-glands of Reinke.

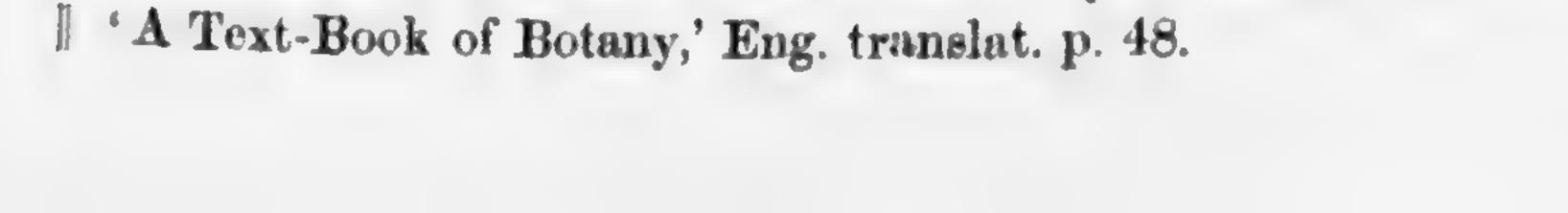
Development of the oil.—In the youngest condition in which I have been able to examine the leaflets, *i. e.* when the food-bodies are only 05 millim. in length, no oil is visible; there is merely a cell-sap cavity surrounded by yellowish protoplasm. I cannot be certain at what age the oil first appears; in food-bodies a little over a millimetre in length (a full-grown one measuring about 2 millims.) a considerable quantity of oil was found. In these specimens there was a cavity in the cell which contained no oil; nor were its walls smooth and rounded like those of the cavities in which oil is embedded in a protoplasmic matrix, but showed rather a jagged outline. This cavity of course diminishes in size as oil is developed in larger quantities in the protoplasm enclosing it; possibly oil globules may escape into it like a secretion into a duct. In sections taken from a young food-body about a millimetre in length, the protoplasm enclosing each cell-cavity is seen to contain

\* Göttingen Nachrichten, 1873, p. 825.



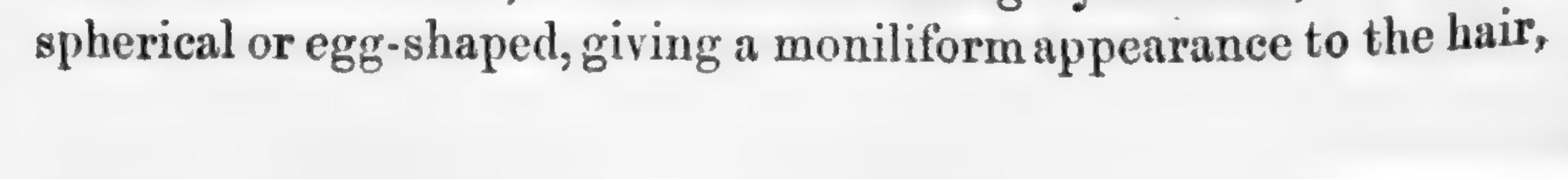
embedded init a row of spherical bodies; they are about 0032 millim. in diameter, and of a dingy yellow colour. As the oil is formed they disappear; but their pigment, no doubt, gives the golden tint to the young food-bodies, and its subsequent absorption causes the change to dull white observable in the older ones. There can be no doubt that they are chlorophyll-bodies which have never developed beyond their early yellow stage; and, from the manner in which the oil takes their place, I believe that they are actually converted into that substance. This phenomenon is not abnormal; for oil is formed in the chlorophyll-bodies of Allium cepa\*. Again, chlorophyll-bodies may be absolutely converted into what should be normally a contained product, as in the case of the starch-grains mentioned by Sachs+. It is not meant that all the oil is produced by the transformation of chlorophyll; it is doubtless also secreted as droplets in the protoplasm. Indeed the latter mode of formation is far more in accordance with the supposition that the food-bodies were originally glandular; for Hanstein ‡ has shown that most resins and balsams are secreted as minute drops in a vacuolated protoplasm of the glandcell. It also corresponds with the formation of animal secretions, e. g. of the oil in the sebaceous-gland cells. On the other hand, the transformation of the chlorophyll into oil may perhaps correspond with another form of secretion of the same substance in the animal kingdom, viz. in the mammary gland. In his paper§ on the mamma, Dr. Creighton shows that the formation of fat in a mammary cell is essentially a process of endogenous cell-formation, the old cell giving birth to a new protoplasmic mass which is entirely converted into oil. Now, in reference to the origin of chlorophyll-bodies, Sachs remarks ||, "it can to some extent be compared to the process of free-cell formation;" so that if I am right in supposing that the chlorophyll is transformed into oil, it will agree with the formation of the fatty part of milk, in its essential feature of being a cell-formation. At the risk of appearing fanciful I may note that the colostrum, or first milk, is yellow from hæmoglobin, the respiratory pigment of animal life; and in the same way the young food-bodies are coloured yellow, the respiratory pigment of plant-life.

- \* Sachs, ' Physiologie Végétale,' p. 354.
- + 'A Text-Book of Botany,' Eng. translat. p. 49.
- ‡ Bot. Zeit. 1868, No. 43.
- § Reports of the Medical Officer to the Privy Council, 1875, No. vi. p. 171.

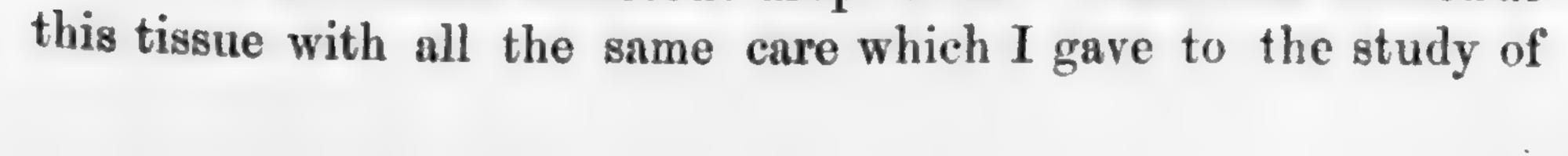


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The nectar-gland.—The gland which secretes the nectar is situated at the base of the petiole; in form it somewhat resembles a flat thorn, such as those on roses with the top cut off. The gland is shown in g g in fig. 1. Its profile outline is there seen to be something like that of a volcanic mountain; and it very well deserves the name of "crater-formed" gland, applied to it by Mr. Belt. The crater is a long narrow trough running along the ridge-like summit of the gland; and into this trough the nectar wells up from the subjacent secreting tissue; in my plant the secretion was so abundant as to drip on to the floor of the hot-The gland, which projects about 2 millims. above the surhouse. face of the petiole, has a curious look of having been thrust into a cleft in the stalk of the leaf; this arises from the fact that the stalk is traversed by a longitudinal groove, and that it is from the base of this groove that the gland arises as an excrescence; and as it grows up between the walls of the groove, it seems to come. through a split in the petiole. In transverse sections perpendicular to the axis of the petiole it may be seen that the epidermis of the gland is continuous with that of the stalk, also that fibro-vascular bundles run up on each side of the central mass of glandular tissue. The latter is flaskshaped in transverse section, the neck terminating above in the crater, and the body resting on the upper surface of the petiole. The glandular tissue is made of loose elongated cells, which are bilaterally symmetrical about a central line, from which they radiate outwards and downwards. CECROPIA PELTATA (the Imbauba tree).-I have already quoted enough from Fritz Müller's interesting paper to explain the relations existing between this tree and its army of ants. The following is his account of the food-bodies. At the base of the leafstalk is a flat cushion, which is raised about 1 millim. above the surrounding parts, and embraces fully one half of the leaf-stalk. While this cushion is protected by the ensheathing ocrea it is white, but becomes brown on exposure to the air. This cushion is absent on young plants, and also on the first leaves of small branches. As the leaf develops, the cushion appears as a white shining silky patch of projecting unicellular hairs; among these spring up crowded multicellular hairs which soon outnumber the simple ones. The former attain a length of 1 millim., and consist of about twelve cells, the lower ones being cylindrical, the upper



which terminates above in a sharp point. When the sheath of the leaf is nearly open, pestle-shaped bodies develop in the cushion; they are from .8 to 1 millim. in length, and from .3 to .5 in breadth; the free end is rounded; and the point of greatest thickness takes various positions; so that they may be either eggshaped, cylindrical, or pear-shaped. When ripe they are milkwhite and rather translucent; on drying they become yellowish and shrink somewhat. As they ripen they project beyond the hairs. They now break off at the slightest touch, and ultimately fall out spontaneously. The growth of fresh bodies continues for several weeks; and on an Imbauba tree that has not been visited by ants, as many as sixty or a hundred food-bodies may be seen projecting from the cushion. F. Müller also gives an interesting account of the ant army gathering its harvest; he carried home with him a branch inhabited by a small colony, hardly numbering a hundred. He removed the sheath from a pulvinus, so that from fifty to a hundred fresh food-bodies were exposed. The harvest was discovered almost immediately, and each ant seized one of the little bodies with its mandibles and dragged it off to the nest. The looser bodies were easily disposed of; but those which were somewhat more firmly attached, cost much time and trouble, and were only loosened by a great deal of pulling to this side and that. In ten or fifteen minutes, only four food-bodies were left; and on these various ants had in vain tried their strength. Fritz Müller supposes that the cushion protects the food-bodies from drought, and from the too early visits of the ants. Is it not possible that it may serve to protect the young bodies from the ravages of slugs? The most watchful ant-sentinel cannot be expected to guard against the night attack of such an enemy; but the cushion of sharp hairs would certainly keep off soft-bodied creatures, acting in the same way as the cinders on a flowerbed. Minute structure.—The food-bodies of Cecropia are composed of a mass of cells continuous with the parenchyma of the pulvinus and included within the epidermis. They do not include any fibro-vascular bundles. The manner in which nutriment is stored in the cells of the food-bodies of Cecropia is essentially the same as that already described in the case of the Bull's-horn Thorn; that is to say, the cells contain a very granular protoplasm, in which are embedded numerous drops of oil. I have not worked at

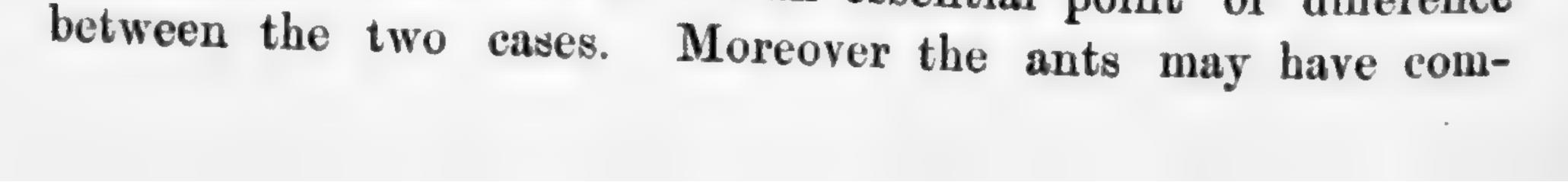


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the Acacia. But as far as my work goes, I know of no essential feature by which a food-storing cell of *Cecropia* can be distinguished from the similar cells of the Acacia.

Development.-By cutting sections perpendicular to the free surface of the young pulvinus, food-bodies in various stages of growth are included in the preparations. The youngest condition in which I have found these structures is that of slight excrescences above the surface, included within the epidermis, and formed of cells differing in shape and in their granular aspect from the ordinary chlorophyll-bearing parenchyma-cells of the pulvinus. This condition of things is shown in fig. 5. These excrescences increase in size, projecting as dome-like masses, and gradually assume the characters of food-bodies. It is this method of development which induces me to believe that the food-bodies of Cecropia, like those of Acacia, are of glandular origin; for it corresponds with the mode of growth of other glands-for instance, those of Dictamnus fraxinella (Sachs, 'Handbook,' p. 114). I am aware that what I have said must seem but slender evidence of the glandular nature of the food-bodies of Cecropia; it is, however, the only view of their homologies which I have been able to form.

If the view here advocated be the correct one, it completes in a curious way the parallel between Acacia and Cecropia; moreover it renders the whole case more intelligible from the evolution stand-point. It is probable that the food-bodies of Acacia were originally glands whose function, like that of the serrationglands of Reinke, was to lubricate the young leaves. But even granting this, it is not easy to make out the steps by which they could be converted into stores of nutriment. I believe that a possible explanation may be found in an observation of Reinke's. He noticed that the glands on the footstalks of Prunus avium (which, from their position, must correspond with serration-glands) secreted nectar, and that the glands on the two or three lower teeth of the leaf occasionally produced nectar instead of their normal secretion (resin). Why, therefore, should not the glands in which the food-bodies presumably took their origin have suffered a similar change, so that oil was formed in the cells instead of sugar or resin? The storing of a product instead of its elimination from a cell is not an essential point of difference



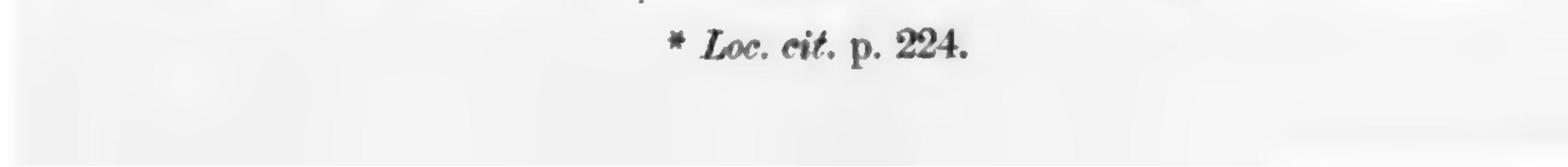
menced a habit of visiting, and probably of protecting, the tree when the glands were in an excretory stage of development; for we know that the nectar-glands on Passion-flowers, according to Mr. Belt\*, serve to attract the small black ants who guard the tree from other creatures.

## APPENDIX.—On the Nectar-glands of the Common Brake Fern (PTERIS AQUILINA).

Since reading the paper to which the present remarks are appended, an observation has been made which, apart from some interest of its own, has a direct bearing on my views as to the

origin of food-bodies.

On June 5th I noticed the presence of smooth green prominences at the base of the fronds of the common Brake Fern. Further examination showed them to be secreting glands, producing a sweetish fluid which exudes from their surfaces. The glands are busily visited by more than one kind of ant, especially by Myrmica; they are also attractive to Elater and another kind of beetle. The gland is well developed while the fern is still very young, and it ceases to secrete when the plant becomes mature. The glands are shown in fig. 6 at g g, the latter being merely seen in profile. In the young state the gland is a fairly conspicuous triangular prominence, standing out clearly from the pubescent surface of the plant. As each frond is fully developed, the gland at its base becomes gradually flattened, and ceases to be so conspicuous. I have not yet been able to examine the minute structure of the glands. The glands have a remarkable power of secreting rapidly. The following observations on this point were made by my father. June 8th. "Examined several ferns with Myrmica on them, and found the glands quite dry. Brushed off the ants, and in from 5 to 6 minutes distinct drops of secretion were formed." On the same day he repeated the observation, and found that the drops of secretion were, as before, reproduced in 6 minutes. The method adopted by the ants to obtain the nectar is in accordance with this high rate of secretion; they may usually be found seated patiently on the glands, evidently sucking up the secretion at fast as it is produced. In many glands shallow excavations are found which appear to have been gnawed; and this is probably the work of the ants. If this be so, it has an interesting



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bearing on *Cecropia*. I have already expressed the opinion that the food-bodies of this plant aboriginally existed as secreting glands, and that by the retention of the secretion they were developed into food-bodies. Now in the fern we have an intermediate stage, a true secreting gland, which is, at the same time, gnawed. If in this case the secretion were to be retained, the gnawing would be probably continued, and the glands would thus be converted into rudimentary food-bodies.

The existence of the secretion in the fern is also of interest in another way. I believe that the food-bodies of the Bull's-horn Acacia are developed from embryonal glands at the tips of the leaflets. I was convinced that those of *Cecropia* are likewise homologous with glands; but I was unable to hear of any case in which such structures are situated at the base of a petiole or branch. The fern shows us that a secreting gland may be found in such a situation. In Delpino's paper on Extra-floral Secreting Organs \* there is no mention of the glands of Pteris Aquilina, nor, indeed, any allusion to the production of a sweet fluid by any cryptogamous plant. It is probable therefore that the functional significance of this organ has not been noticed. In the same paper Delpino states his view that whenever a sweet fluid is secreted elsewhere than in the floral nectaries, it serves as a protection to the plant by attracting ants, which keep other creatures away, just as occurs with the Bull's-horn Acacia, and the Passion-flower mentioned by Mr. Belt<sup>+</sup>. The fact that the fern secretes a sweet fluid seems strongly opposed to such a view; for this plant is sin-

gularly free from enemies, not being eaten by the larger animals, by rodents, or by grasshoppers.

In the fern the secretion of a sweet liquid is decidedly connected with the growth of the young fronds; for it ceases when they are mature. Again, the honey-like fluid on the stipules of *Vicia* sativa has been shown by my father to be secreted only while the sun shines on them. It appears that, in these cases, the secretions are dependent on the continuance of active vital or chemical changes in their immediate neighbourhood. They seem, in fact, to be of the nature of excretions, waste products utilized as food by the ants in the same way that the sweet excretion of the Aphis is made use of by them.

> \* Bullettino Entomologico, 1874. † Loc. cit.

### DESCRIPTION OF PLATE VI.

- Fig. 1. A small branch of *Acacia sphærocephala*, natural size: *h*, *h*, *h*, *the* hollow thorns; *g*, *g*, the nectar-secreting glands.
  - 2. Part of a leaflet of Acacia  $(\times 5.7)$ :  $f^1, f^2, f^3$ , the three lower foodbodies on one side; p the dwarfed point of the upper leaflet corresponding to  $f^3$ .
  - 3. Transverse section of food-body of *Acacia*, treated with solution of potash to show the oil globules. (Hartnack No. 8.)
  - 4. The same, treated also with creasote and turpentine (Hartnack No. 8) to remove the oil and show the protoplasmic matrix.
  - 5. Cecropia peltata. Development of a food-body. (Hartnack camera lucida with objective No. 5.)
  - 6. Young plant of common Brake Fern, Pteris Aquilina, showing the nectar-

glands,  $g^1$ ,  $g^2$ .

## Lichens collected by W. POOL, Esq., in Madagascar. By the Rev. J. M. CROMBIE, F.L.S.

[Read June 1, 1876.]

JUDGING from its climate and situation, there can be no doubt that the island of Madagascar possesses a very rich and extensive lichen-flora. Unfortunately, however, it is still in this respect almost entirely a *terra incognita*; nor does the present small collection throw much light upon its lichen treasures, though it affords some indications that these are both valuable and varied. No habitats are attached to the specimens, all of which were gathered near Antananarin, the capital of the island; but it may be presumed that they are entirely corticole.

## SPHÆROPHORON MADAGASCAREUM, Nyl., sp. n.

"Thallus albidus, erectus, compressiusculus (latit. fere 1 millim. vel angustior, crassit. 0.2 millim. vel etiam tenuior), dichotome divisus, evernioideus (altit. circiter 3 centimetrorum vel minor); apothecia primum in globulo thallino albo inclusa, deinde globulum nigrum nudum fingentia (latit. 0.5-0.7 millim.); sporæ 8næ, globosæ, diam. 0.004-0.005 millim. Species omnino distincta, nulli alii affinis."--Nyl. in litt.

The thallus is somewhat glaucescent above, and beneath more purely white. Occasionally, as in the other species of the genus, it is more or less tinged of a reddish or pink colour. From all of these, however, it differs very remarkably in the situation of the apothecia, which are not terminal on the apices of the primary axes, but sectored which are not terminal on the apices of the primary

ares, but scattered chiefly towards the extremities of	i the brai	ncnes.
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