rable geometer, and a minute analysis of his works; perhaps might be added some brief articles by very illustrious living mathematicians; something, in fine, which would be as a funeral crown offered to the memory of the great dead.

[Written by Juan J. Durán-Loriga for *Le Matematiche*, and translated by the English editor G. B. Halsted.]

THE EXTRA-NUPTIAL NECTARIES IN THE COMMON BRAKE, PTERIDIUM AQUILINUM.

THE common brake, *Pteridium aquilinum* Kuhn (*Pteris aquilina* L.) has for a number of years been used in educational institutions in this country as a laboratory type, more especially in connection with introductory courses in general biology in which both animal and plant types are used. That the presence of nectar-secreting organs in this form, therefore, should have been so generally overlooked as the writer has been led to believe, the more especially as they were made known to the botanical world as early as 1877,* is a matter of some surprise.

It is our purpose by means of the present paper to review the facts already published, and to present them, together with the writer's own observations, in order to draw to the attention of teachers of biology the fact of the presence, in a non-flowering plant, of an organ such as is thought of usually in connection with the phanerogams alone. Interest attaches to this structure, also, from the fact that a definite organ of secretion may be observed by students in a much-used laboratory type, thereby enhancing its value as such.

The extra-nuptial nectaries in *Pteridium aquilinum* were discovered by Francis Darwin (*l. c.*), and their microscopic appearance was briefly described by him in 1877. The possible biological meaning of these organs was also discussed.

Two years later, Bonnier* pointed out the presence of similar structures in certain genera of ferns, namely, in *Cyathea*, in *Hemitelia* and in *Angiopteris*, and briefly described some points in their anatomy. In addition, this author examined the nectar of the plant here under discussion.

In 1891, in view of the scanty description till then extant, W. Figdor† published a fuller account of the nectaries in *Pteridium*. This description includes the external appearance and the histology of the gland, and is accompanied by two illustrations. Later in the same year Figdor's paper was reprinted, accompanied by some notes and one illustration‡ additional, by H. Potonié. §

EXTERNAL APPEARANCE.

The nectaries in *Pteridium aquilinum* occur on the fronds at the bases of the pinnæ and pinnulæ on the morphological lower side of the leaf. The largest and most conspicuous are the lowermost, that is, those at the bases of the first pair of pinnæ. On one developing frond, therefore, one may observe a complete developmental series. When examined macroscopically the glands appear as approximately oval areas just below and extending somewhat into the angles formed by the mid-veins of the first and second, and second and third, orders. The external surfaces of the glands are smooth, because of the absence of the chaffy scales found elsewhere on the young frond.

* Darwin, Francis. *Jour. Linn. Soc.* **15**: 407. 1877.

* Bonnier, G. 'Les nectaires.' Ann. Sci. Nat. Bot. VI. **8**: 5-212. 1878.

† Figdor, W. 'Ueber die extranuptialen Nectarien von *Pteridium aquilinum*.' Oesterr. botan. Zeitschr. No. 9. 1891.

‡ Reproduced in Engler and Prantl's 'Natürlichen Pflanzenfamilien,' 1^4: 67.

§ Potonié, H. 'Die 'extranuptialen' Nectarien beim Adlerfarn.' Natur-Wiss. Wochenschr. **6**: 401. 4 O. 1891.

Their color, according to Figdor, is brown-red in the central part of the nectarial surface, developing into red on the edges. Darwin's statement is that they are 'smooth green.' In our east North American plants, the color in the young state is much as described by Figdor. Later the red color is lost, and the organs are then deep green. Darwin's and Figdor's statements may, therefore, be harmonized as they appear to apply to different stages of growth, if indeed the European plants do not differ among themselves and from the American. Figdor further notes that the membranes of the nectaries early become brown and that, later, they thicken considerably. The use of the red color is quite problematical.

The secretion of nectar is very abundant during the unfolding of the frond. So abundant is it, in fact, that large beads of the limpid fluid may be seen from a distance, resting on the nectaries or running down the petiole. With a hand lens, one may easily note the accumulation of nectar after the surface has been wiped off. Darwin found that a drop of the liquid was formed in six minutes. Handling and tasting the secretion shows it to be sirupy and very sweet. According to Bonnier (*l. c.*) the sugars saccharose and glucose are present. Here, as in analogous organs in other plants, the exudation is quite independent of bleeding pressure. Leaves which have been broken off continue to produce nectar for some days, provided, of course, that they be kept in fair condition. As the frond ages, the activity of the glands is lowered, until they finally cease to secrete and become functionless as nectaries.

ANATOMY.

The epidermis consists of polygonal cells, with a depth that is greater by about one-third than that of the rest of the epidermal cells of the petiole; in transverse section they are nearly square (Fig. 5). These cells have red coloring matter in their sap, although the color is not confined merely to the glandular areas, but is usually extended from them in bands of various breadths up and down the petiole. The loss of this color as the age of the leaf increases has been noted above.

Scattered here and there on the surface are a number—a dozen or more—of stomata. These are irregular in position, in surface view very much rounded (Fig. 1a), resembling in this respect very closely the water pores of the garden nasturtium (*Tropaeolum* sp.).

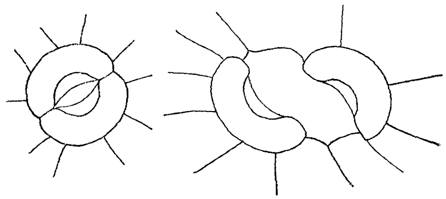

FIG. 1a. Stoma from nectary.
FIG. 1b. Stoma in which the guard cells have been spread apart by growth of the surrounding tissues.

They do not, however, lack so entirely the characters found in air stomata, as is shown in the figure. The delicate hinge mechanism is not present, and the thickening of the walls is even all around, in which the stomata agree in essential detail with water stomata, such as are found in *Secale cereale, Conocephalus ovatus* and other plants.

In some cases the stretching of the epidermis incident to growth causes a displacement of the guard-cells (Fig. 1b), and a consequent enlargement of the pore. The guard-cells are raised above the general surface (Fig. 2), in which particular the writer's observations fail to coincide with those of Figdor, whose illustration in other regards also does not show the guard-cells to possess any characters usually found in such. Figdor states that a 'test with a sugar solution indicated that some of the stomata carry on the usual function while others serve for the exudation of nectar.'

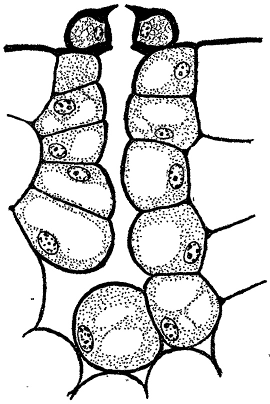

FIG. 2. Transverse section through a stoma and adjacent tissue of the nectary.

It is, however, not clear how the test was applied, and we believe that in view of the facts the question of the function of the stomata may be decided upon other grounds. A very few of these which occur on the edge of the nectarial surface have the appearance of air stomata, but by all odds the big majority have the characters above described, from which it appears that the guard-cells are in such cases quite functionless in opening or closing the entrance. Furthermore, the nectar when it is being secreted is so abundant that it must needs hinder completely the gas interchange at that time. That such interchange takes place later is almost certainly the case, as is indicated by the condition of the chlorophyll-bearing cells of the gland. Nor does the immobility of the guard-cells call for remark, inasmuch as the amount of tissue involved in transpiration coincident with respiration is relatively so very small as to have no effect upon the turgor of the whole leaf. Stomata are absent from the rest of the petiolar surface, excepting that, as Potonié * has pointed out, they are present along two bands on either side of the morphological upper flattened side of the leaf-stalk, beneath which the hypodermal stereome is absent, though elsewhere present except in the nectaries. The relation of these bands to the glands should here be pointed out. As just stated, the rachis possesses two such bands, which pass *without dividing*, each along the lower margin of one of the first pair of pinnae. The band lying along the upper margin of a pinna and that along the side of the rachis nearer the same and above its insertion arise *at the same point*. At this point lies the nectary. These relations, which are exhibited in Fig. 3, *a* and *b*, are repeated at each fork in the frond.

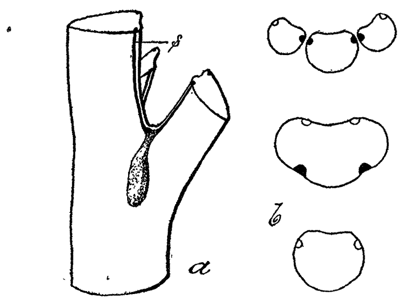

FIG. 3. *a*, lateral view of rachis showing the nectary and the stomatal bands, *s*; *b*, diagrams showing the distribution of the bands.

Through these true pneumathodes, by reason of the anatomical relations just indicated, the gas interchange may easily take place between the glandular tissue and the air. On old dead fronds the nectarial stomata are so large as to be seen with the naked eye, from which fact the presence and extent of the gland beneath may be determined.

Beneath the epidermis lies the glandular tissue extending to a depth of 1 mm. or a fraction more. In a transverse section through fresh material, the extent of the same may be recognized by the deeper green color contrasting with the lighter color of the surrounding tissues. The cells are rounded in form, as described for

* Potonié H. Jahrb. des Königl. bot. Gartens zu Berlin, **1** : 310-317. 1881.

Hemitelia by Bonnier (*l. c.*), and contain relatively much more protoplasm than the contiguous cells, large nuclei and chloroplasts. The cytoplasm is vacuolated and the cell walls are thin. The cells stand in contrast with the ground parenchyma on account of their smaller size, their diameters being between the ratio of 1 to 3 and 1 to 4. The cells near the epidermis are larger than those lying deeper in the gland. In making the foregoing statement, we differ from Figdor, who says "The single elements of the gland are about the size of the cells of the fundamental parenchyma." Frequent small intercellular spaces occur. These connect with each other and finally with the substomatic spaces which are of considerable size (Fig. 2). Through these, therefore, the secretion may find its way to the surface of the gland. Bonnier, in the paper above cited, makes no mention of the substomatic spaces in the special treatment of the ferns. Further on, however (p. 151), he makes a general statement to the effect that he had established the fact that, in the cases of nectaries with stomata, these are either without a substomatic space or have only very small ones. His figure representing the nectary of *Hemitelia obtusa* (on his Pl. 1, Fig. 9) certainly bears out his general statement. We cannot, however, regard this figure as satisfactory. No attempt was made to delineate the stomata, except in very schematic fashion, on account of the small size of the drawing, for which reason also the possibility of representing substomatic and intercellular spaces was very much lessened. The presence of a large substomatic space, however, may not be regarded as of any importance in the economy of such an organ as a nectary, in which the movement of the fluid is the important and characteristic feature.

Passing on to consider the relation of the nectary to the vascular tissue, we notice in the first place the distribution of bundles in the immediate vicinity of the former. Fig. 4 shows, in diagrammatic form, this relation, from which there appears to be little variation to be noted beyond. A broad

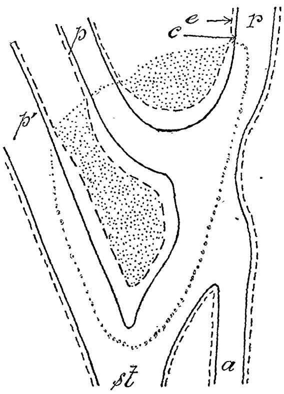

FIG. 4. Diagram showing the relations of the vascular tissue and gland. The dotted outline shows the extent of the latter. *c*, limit of the cribral part of the bundle; *e*, endodermis. The pericycle is included between these.

stele* (*st*) divides at the lower angle of the nectary, one branch (*p'*) running along one side of the gland and thence into the pinna, the other and larger passing along the other border of the gland, broadening as it goes into a vascular plate which consists of a dense complex of short, irregular wood elements, well-developed cribral cells and a several-layered pericycle, to be described below.

From this plate of vascular tissue, which lies beneath and somewhat obliquely across the nectary, pass forward two branches, *p* and *r*, which go into the pinna and rachis, respectively. Sometimes four branches arise by the splitting of these two, but the general character of the arrangement is quite constant. Sometimes a small stele runs into the complex, as shown at *a*, Fig. 4.

* The term stele is used here, in the ferns, without reference to the question of morphological propriety. See Jeffrey, E. C., 'The morphology of the central cylinder in the angiosperms,' *Trans. Can. Inst.*, Vol. 6.

In no case examined, however, does a bundle end in a gland, as held by Figdor (*l. c.*). The relations of the glandular and vascular tissues are none the less intimate and striking, as we shall see in coming to the second point.

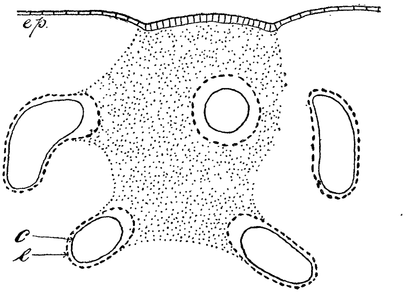

FIG. 5. Diagram of a transverse section through a nectary. *ep*, epidermis ; *c* and *e*, as in Fig. 4.

In examining a transverse section we see the glandular tissue extends towards and comes partially to surround the vascular bundles adjacent (Fig. 5), and, further, that the pericycle of these bundles, in the regions contingent upon the gland, consists of three to four layers of enlarged cells, and not, as is to be found elsewhere, of a single layer of cells (Fig. 6, *a* and *b*). These enlarged pericycle cells are abundantly supplied with cytoplasm of fine, tenuous structure with large and often irregularly shaped nuclei. The cytoplasm is little vacuolated.

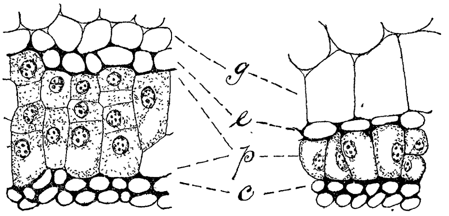

FIG. 6. *a*, transverse section through a portion of the pericycle in contact with the glandular tissue. *b*, a similar portion in a bundle adjoining the ground tissue. *c*, cribral cells ; *p*, pericycle ; *e*, endodermis ; *g*, ground parenchyma.

The pericycle cells found elsewhere in the petiole, where the glands are active, are supplied with a scant amount of cytoplasm. The endodermis,* which is usually regular and well marked, is, in the vicinity of the nectary, quite irregular and often difficult to recognize, and its cells have very much the character of the adjoining gland cells in shape and content. We may thus regard these cells, namely, those of the endodermis and pericycle, where the bundles and nectary touch, as a part of the gland. Whether we may assign a different function or the same to these cells may not be answered. Bonnier (*l. c.*) has indicated that, besides the two sugars above named, an invertin is to be found in the gland. The suggestion occurs to us that this substance originates in the pericycle. Nevertheless, the greater development of the pericycle as already indicated can perhaps be entirely accounted for by the activity of its cells in passing the soluble carbohydrates from the moving sap into the gland.

After the activity of the gland ceases, the thickening of the walls of the endodermis commences, in all the bundles lying in the petiole near the fork formed by the pinna, and the process extends to the surrounding parenchyma. In this way the strength of the fork is very materially heightened. We notice also, with Figdor, a thickening of the walls of the gland cells, a process which takes place in all the chlorophyll-bearing cells beneath the stomatal bands.

In offering a teleological explanation of the organs above described, F. Müller pointed out that in Brazil the fern is visited by an ant (*Cremogaster* sp.) of which a leaf-cutting species, an *Oecodoma*, stands in dread. To this Francis Darwin † answers that the plant has few natural enemies—meaning, presumably, in England, though this is equally true, so far as observation goes, in North America. Francis Darwin further suggests, in the view of the possible weakness of the above explanation, that the

* Derived from the phloeoterma of Strasburger.

† *Nature*, **16** : 100.

gland is either an organ which was formerly of use and is now passing away, or that it is connected 'with some unknown process of nutrition.' That its activity 'is decidedly connected with the growth of young fronds' stands in favor of the latter view. A supplementary suggestion has already been made by the writer to the effect that the solution of actively secreted sugar may act as a carrier for some other substance in the nature of an excretion.*

The writer has observed on the surface of the gland in some cases a felt of dark-colored fungal hyphae. The occurrence of these, when the leaf-blade has not yet unfolded, carries with it the suggestion that the nectarial surface is a constant infection-point, the sugary fluid acting as a nutrient medium and the entrance of the hyphae being made easy by the large stomata.

ORIGIN OF THE NECTARY.

Certain facts which have been pointed out give us grounds for offering a view of the origin of the nectaries, to the effect that they have arisen as portions of the respiratory areas of the petiole and its branches, which have become secondarily specialized as nectar-secreting glands.

In support of this view, we recall the relation of the nectaries to the stomatal bands (pneumathodes), with which they have a practically identical structure, with, however, a more intimate connection with the vascular system. We regard the wide distribution of these band-shaped pneumathode regions in the ferns as indicating a phylogenetically greater age than that of the nectaries as such. If this be true, Francis Darwin's suggestion, quoted above, that the nectary is an organ once useful but now on the wane, must probably be thrown out of court, though not necessarily. Further, the stomata, while clearly functionless as pneumathodes during the period of the gland's activity, and deprived of the delicate mechanisms for closure both by their own development and the manner of growth of the surrounding epidermis, are nevertheless to be regarded as respiratory mechanisms, serving the function of setting free the nectar. The analogous conditions in *Tropaeolum* and other plants may be cited as a parallel case save in the nature of the exudate. The presence of the sub-stomatic spaces, usually broader beneath the stoma than represented in Fig. 3, together with the intercellular spaces both suggest the same thing.

It is to be questioned if the presence of chlorophyll in the gland has any necessary relation to the activity of the organ as a gland, upon which point further study of the cytological phenomena may throw light.

Haberlandt* has drawn the provisional conclusion with regard to nectaries in general, that they have been derived phylogenetically from hydathodes. In summarizing the present paper we submit the case described herewith as one in which the nectaries have been derived both ontogenetically and phylogenetically from pneumathodes.

FRANCIS E. LLOYD.
TEACHERS COLLEGE,
COLUMBIA UNIVERSITY.

* Bonnier (*l. c.*) has shown that other substances are thrown off in small quantities.

* 'Physiologische Pflanzenanatomie,' p. 432.

THE BRITISH NATIONAL ANTARCTIC EXPEDITION.†

THE resignation of the man who is, before all others, fitted to be the Scientific Leader of the National Antarctic Expedition will lead the fellows of the Society to expect some statement of the causes which have produced a result so disastrous to the interests of science. The following statement gives an account of the efforts which

† A letter addressed by Professor Edward B. Poulton, of Oxford University, to the fellows of the Royal Society.