THE EPIDERMAL ORGANS OF PLANTS

THEIR MORPHOLOGY AND PHYSIOLOGY

BY

CHARLES F. COX, F. R. M. S.

VICE-PRESIDENT OF THE NEW YORK MICROSCOPICAL SOCIETY, CORRESPONDING MEMBER OF THE SOCIÉTÉ BELGE DE MICROSCOPIE, ETC., ETC.

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The Epidermal Organs of Plants.

It is, of course, well known that those parts of plants which are exposed to external influences—to light, heat, evaporation, etc.—become compacted and hardened into a rather dense and rigid tissue called the epidermis. This differentiation is not well marked in roots and submerged parts of aquatic plants, but even in such parts we recognize at least a theoretical difference between the most exterior layers of cells and those of the so-called parenchyma lying beneath.

Upon the aerial portions of plants there is generally a tissue external to the epidermis—of the nature of a very thin, usually homogeneous and transparent pellicle or skin,—termed the cuticle.

The epidermis, however, may be regarded, physiologically, as the most external organized and organ-producing substance of the plant.

From this epidermis are developed all external appendages, known as hairs, villi, papillæ, tentacles, bristles, thorns, scales and glands, with analogous and homologous organs, including probably the sporangia of ferns, and even the ovules of phanerogams.

It has been proposed to class all such lateral growths from the epidermis under a single name: Trichomes. This grouping, however, not being entirely satisfactory in all respects, is merely tentative; and there is good reason to think that, when microscopical botany has been thoroughly worked up, the whole theory of the epidermis and its appendages will have to be reconsidered and much modified.

Hairs are the most attractive of the epidermal appendages, and are exceedingly varied in form, as well as often charmingly beautiful in appearance. They have long been favorite objects of observation with microscopists, though I cannot say that they have long been objects of scientific study and investigation; for, as far as I am aware, they have seldom attracted attention except for their external symmetry and beauty.

This mere prettiness of plant-hairs cannot be adequately expressed in description; and, so far from wondering that it has attracted attention, I am surprised that it has not attracted more; for I am sure that no class of microscopic objects offers more various beauties of outline, ornamentation and color, than do these exquisite gems of the vegetable world.

The outlines of different kinds of plant-hairs have often been figured, and I will not consume time and space in any attempts at an extended description here. It may be well, however, to mention the more characteristic forms.

To begin with, we have what may be called the right hair, which is a simple, perpendicular, or more or less appressed, unicellular growth, such as may be found on *Lithospermum hirtum* or *Lithospermum canescens.*

Jointed hairs are similar in outline to the right hairs; but instead of being unicellular, they are composed of a series of cells or nodes. Such hairs are found upon many of the

Compositæ,—for instance, *Pluchea bifrons.*

In segmented hairs the component cells are separated by deeper constrictions than in jointed hairs ; and they resemble, when filled with their living fluids, strings of translucent beads. Such hairs grow upon the stamens of *Tradescantia Virginica* and upon the leaves of *Polemonium cœruleum.*

Cleft hairs resemble right hairs which have been split part way down, and the separated portions of which have become more or less depressed. In some cases this depression proceeds so far that the hair appears to be a long, doubly terminated, horizontal cell attached to the leaf by a pedicel at its centre. Such hairs may be seen on the leaves of *Clematis erecta, Astragalus vesicarens,* and of *Benthamia fragifera.*

Branched hairs are multicellular hairs in which growth takes place in many directions, or not entirely in one general direction. Examples of this mode of growth are found upon *Alternanthera lanuginosa,* and upon *Verbascum thapsus* and many others of the Scrophulariacæ.

A variety of this species is the radiate, in which the branching is confined to nearly horizontal planes. This form of hair occurs upon the upper side of the leaf of *Shepherdia Canadensis,* and upon many of the Polypodiaceæ.

These branching modes of growth (especially the radiate) give rise to many of the forms commonly included under the term *stellate ;* but I prefer to reserve that name for unicellular, star-shaped hairs, such as are found upon *Deutzia, Vesicaria* and some species of *Alyssum.*

Peltate hairs are those partly membranous, partly radiate, scale-like hairs, which occur upon all the *Elæagnaceæ,* upon some of the *Crotons* and upon *Sida lepidota.*

I apply the term rosette to those less scale-like, though nearly peltate, hairs such as are found upon *Croton caramba.* These differ from the peltate hairs in having fewer lines of radiating growth, and in being less membranous or scale-like. They approach closely to the forms of the glands of *Callicarpa,* of *Carya,* or of the Myricaceæ.

When several simple hairs are developed from adjacent epidermal cells, I term them grouped. Sometimes these grouped hairs consist of but two simple hairs in contact at their bases, but often five or six or more form a group which, when seen from above, give the appearance of a stellate form. Such stellately grouped hairs are common among the Malvaceæ and the Cistaceæ. In *Helianthemum canum,* var. *genuina,* we have a good example of stellately grouped, short hairs, associated with simple groups of two, three or four long right hairs.

Closely allied to this form is the one which I call mammillate. In this species what would be the central hair of a group is fully developed, but the surrounding epidermal cells are only partly developed into hairs, most frequently just enough to slightly raise them above the general surface of the epidermis, thus producing a protuberance or mamma upon the surface of the leaf, from the centre of which the fully developed, simple hair seems to spring. This is a characteristic form amongst the *Borraginaceæ,* and is most strikingly exhibited on the leaf of *Onosmodium Virginianum.* In some species, however, all the hairs are aborted, and what might otherwise be a group of hairs, is only a group of partly developed epidermal cells. This is exemplified in *Echinacea angustifolia.* On the other hand, it happens in some species that all the grouped epidermal-cells, or a large number of them, become fully developed hairs, but only the central one grows perperpendicular to the surface of the leaf, the others radiating about its base in a nearly horizontal position, or at an acute angle to the surface.

A fine example of this is seen in *Onosma montana.*

Among the Compositæ a very striking, but not a very common, form of hair is what may be called serrate. In its simpler variety its outline somewhat resembles that of wool; but in its more pronounced phase it suggests the hair of some animal among the rodents, particularly of the Indian bat. This is the case with the leaf-hairs of *Hieracium tomentosum* and of *Adenostyles lanatus.*

Glandular hairs (hairs bearing glands at their extremities) are found upon a large number of plants, particularly upon the so-called "insectivorous" plants, and also upon many others which possess glands rather for the purpose of secreting or excreting than for absorbing, such as the tomato and *Rhodora.*

Tentacular hairs are the most differentiated and specialized of all,—they being endowed with the power of movement in response to stimulation, besides the power of secreting and absorbing. These are best exemplified in the Droseraceæ.

At the other extreme of the scale of development are what I term papillæ, which, together with what may be called villi, are perhaps not so much of the nature of immature or undeveloped hairs, as of organs intermediate between hairs and stomata. Instances of the occurrence of these forms—which are hard to separate, the latter being apparently only less differentiated than the former—may be found on many of the *Ericaceæ,* particularly on *Rhodora Canadensis* and *Rhododendron Nuttallii,* and also on *Clematis recta* and on *Porsooni salicina.*

There are, of course, many other forms of hairs, some of them intermediate varieties to those I have named, and some of them connecting links between hairs and glands or other epidermal organs; and several of these often occur upon the same plant or part of the plant.

It would be an easy matter to arrange a series of specimens showing an almost imperceptible running of one of these forms into another, in perfect gradation all the way from the true sunken gland up to the most developed and specialized forms of radiate, stellate, peltate or tentacular hairs.

The difference between a secreting, glandular hair and a true gland seems to consist mainly in the fact that one is entirely sessile, or sunken, while the other is more or less pedicellate. Sachs states that all reservoirs of oil, resin, gum, etc., whether internal or external, are only slightly different developments of the same organ; but if we include among such reservoirs the turpentine-cells of the Coniferæ, as has been suggested by some writers, we shall have to rearrange somewhat our present ideas of what are epidermal organs.

As may have been inferred from what I have already said, the forms of hairs, glands, etc., are more or less characteristic of families, orders, genera, and in some cases of species even.

This is the most interesting, and scientifically the most important point in this whole subject; but it has not yet been even approximately elaborated, and there is vast room for research here and great promise of valuable results.

Take the forms of hairs peculiar to the Elæagnaceæ, for example, they are as characteristic of the order as any other part of the plant; indeed, in this particular case, I think they are the most characteristic and distinguishing part. And yet little or nothing is made of these microscopical characteristics in classification, although enough has already been learned concerning them to show that they are more intimately connected with the physiological nature and natural affinities of the plant than are many less intrinsic qualities or characters, which are given a prominent place in the usual system of classification. To be sure, reference is sometimes made to the "silvery" appearance of some species, and to the "scurfy" appearance of others, to the naked eye, but the characteristic feature of *Shepherdia* or *Elæagnus* or *Hippophæ* is seldom even referred to in such botanical works as I have happened to consult.

The hairs of the *Malvaceæ* also are very characteristic. In general, to the casual observer, they seem to come under the very inclusive designation of stellate. But they are not stellate, in the proper limitation of that term, or as the hairs of *Deutzia*, for example, are stellate. In the genus *Sida*, and in one or two other genera, they are what I have called peltate, and in still other genera they tend toward what I have called the radiate form. But throughout the larger part of the order they are what I have termed grouped hairs. Upon the upper side of the leaf they may be grouped only in twos or threes, or the hairs may be even solitary; but upon the under side of the leaf, or upon the calyx, the groups will probably consist of four, five, six or more hairs, disposed in such a way as to give rise to the so-called stellate appearance, although this stellate grouping will often be associated with the simpler aggregations, or with the single right hairs. But a tendency to stellate grouping, in some part of the plant or at some stage of its existence, is decidedly characteristic of the Mallow family as a whole.

In the genus *Althœa* there is a disposition to complexity of form and luxuriance of growth on every part of the plant—even on the petals.

In *Malva* there is less complexity of form and less luxuriousness of growth, the stellate groups being most pronounced upon the calyx.

In *Abutilon* there is still less hairiness and still less tendency to stellate grouping.

In the genus *Hibiscus* the hairs almost disappear from the leaves (especially from the adult ones), though the stellate groups still form rather abundantly upon the calyx and the seed-pod.

These facts are sometimes vaguely referred to in the text-books under the heading of pubescence; but usually *Hibiscus* is spoken of as smooth or glabrous, because the leaf in its adult stage is hairless, or nearly so, to the unaided senses, while the truth is that hairiness in some part of the plant, in some stage of its existence, and, as a general rule, hairiness of a particular kind, is almost if not quite as much a characteristic of this genus, as well as of its order, as are its "alternate, stipulate leaves and regular flowers, with monadelphous stamens."

Nothing can be more characteristic of the Borraginaceæ, as an order, than their hairinesss as seen under the microscope. This is generally of the kind I have described as mammilate; and so striking is this in almost every genus and species I have examined, that the minutest fragment of a leaf large enough to hold a hair, would in most cases be enough to determine at least the order to which it belonged.

Amongst the Cruciferæ, too, there are some very distinct groups of genera marked off by the peculiarities of their leaf-hairs, so that one who has once become familiar with *Alyssum*, *Vesicaria*, *Draba* and *Arabis*, for instance, would have little difficulty in determining the place of a specimen of one of them, by microscopical examination alone. As far as my experience has gone, the grouping of plants by their microscopical characteristics has been found to accord in the main with the classifications already made by botanical science on other grounds; but in running through the order Cruciferæ, for example, one is often struck by the wide dissimilarity discoverable by the microscope, between certain groups of genera; and one is led to wonder whether plants so different in their minute structures can really be near relatives, even though their mode of inflorescence and some other attributes may be similar.

Nevertheless, the microscopical characteristics of plants may be determined and tabulated so as to be of much value for purposes of identification; and I am inclined to think that such labor will some day result in a system by which either extant or extinct orders, at least, can be identified to a certainty; and such a system would be of no little importance in many lines of scientific investigation, as will at once be seen. Thus, in geological science, buried parts of plants would throw light upon the age and character of the deposits in which they were found, and in zoological science even the half-digested food of beasts, birds or insects might be made to disclose the habits of the eaters.

But, as has already been foreshadowed, it is not only the mere form or figure of the hairs that is characteristic. Their distribution upon different parts of the plants is also a matter of regular and peculiar habit, as well as their existence or non-existence at different stages of the plant's history.

In many plants the young leaves or stems are hairy or scaly, while the adult parts are quite smooth.

We recall the fact that the *ramenta* of ferns commonly fall off when the frond is fully developed; and this is also true of the hairs of many phanerogams. But even when the hairs are not shed, the adult leaf will be relatively much less hairy than the young leaf, from the fact that the hairs are developed coincidently with the leaf itself, and that their number does not increase as the leaf increases in size. The same number of hairs is, therefore, spread over a much greater surface in the adult leaf than in the young, growing leaf; and the young leaf is therefore the more pubescent, relatively to its surface. This has an important bearing, as will be observed when I come to speak of the physiological side of my subject. It follows from the fact I have just mentioned, that to obtain the most striking specimens of vegetable hairs, the microscopist generally selects the young, terminal or rapidly growing leaves, stems or petioles.

Another point as to distribution, I have barely referred to already, and that is that even when leaves are entirely hairless the calyx may be hairy. Sometimes this is true of the petals, and often of the filaments. In other words (to generalize these facts), hairiness begins at the growing point, and persists there the longest. It may never exist elsewhere on the plant to any considerable extent, but it is likely to exist upon the part last developed, whether leaf or flower. The hairs may drop off from the older parts, but they are not often absent from the younger parts. This matter also has an important connection with physiological facts, which I shall mention hereafter.

One of the most obvious facts connected with the distribution of hairs is that they are found more frequently and more abundantly upon the under side than upon the upper side of the leaves, the sepals or the petals. This is a very general rule, though there are exceptions to it which seem to indicate that the relative hairiness of the two surfaces of the leaf depends upon the position in which the leaf grows. I am inclined to the opinion that when the leaf naturally assumes such a position that one side receives a much larger amount of light than the other, that side will be the least hairy, if not entirely destitute of hairs, while the shaded side will be the one most favorable to hairiness. In plants whose leaves grow more or less perpendicularly, the difference between the two sides is apt to be less marked.

Heliotropism may affect the relative hairiness of the two sides of the leaf, either in causing a greater difference by presenting one side more constantly to the light, or in causing less difference by presenting both sides equally. It is said that the "compass plant" of our western prairies (*Silphium laciniatum*), always presents its leaf in a plane with the north and south meridian, and both sides of its leaf are alike; but, aside from its heliotropism, this may perhaps be due merely to the leaf's tending to a perpendicular position.

In the Bayberry (*Myrica cerifera*) we find that the upper side of the leaf is the more hairy, while the glands follow the general rule in being more abundant on the under side. But, notwithstanding these occasional exceptions (which will doubtless be found to be explainable in accordance with the general theory), it is a rule that the under side of the leaf, and that which corresponds to the under side in homologous parts, is the hairy side. If both sides are hairy this side will be the more so. This, as I have already said, I am inclined to refer to the influence of light as a general principle, though the fact that the hairiness of sepals and petals is still on the outer side (or the side corresponding to the lower side of the leaf), does not seem to be directly explainable on this theory, but seems to be indirectly connected with it, through the mere homology of the parts.

Another very obvious fact as to distribution, is that hairs are most abundant upon the mid-rib and the larger fibro-vascular veins. When they do not exist at all upon other parts, they are often abundant upon these vessels, and the mid-rib is seldom absolutely hairless. It is one of the most striking points in connection with this subject, that hairs commonly spring from the surfaces of fibro-vascular bundles, or are more or less directly connected with them. In most plants this characteristic is plainly seen, but in many it is obscured by the great profusion of hairs; and in some, though not hidden, it is not marked. I believe, however, that there is an essential relation between hairs and the fibro-vascular system, which I will refer to more specifically by and by.

What I have said as to the distribution of hairs, is generally true also of glands. Indeed, this is to be expected from the fact that hairs and glands are only different developments of the same organ, as it has been already stated.

Glands exist under every form, from a mere epidermal cavity containing an essential oil, as in *Magnolia glauca* (the White Bay), or *Hypericum parviflorum*, to the complexly specialized, secreting and absorbing tentacles of the Droseraceæ. Between these extremes we find a mere orifice emitting a drop of resin or gum—as in *Gaylussacia*—the half-external, half-internal, multicellular, rosette-like gland of *Rhododendron ferrugineum*, the sessile, but quite external gland of *Myrica* or *Callicarpa*, the glass funnel of *Chenopodium*, the pedicellate, spreading, flower-like gland of *Rhododendron Nuttallii;* the short, glandular hair of the tomato or *Rhodora* or of *Pluchea ;* and the long, stinging hair of *Urtica*. As has been intimated already, the hairs of *Croton caramba* and the glands of *Carya glabra* are so nearly alike in appearance that they may be regarded as connecting links.

One of the characteristics of all epidermal appendages is the tendency to a deposition in them of silica or of lime, particularly of silica. In the Diatomaceæ the siliceous frustule is the largest part of the whole organism; and in the Equisetaceæ and the Gramineæ the deposit of silica in the epidermis and cuticle is of no small amount or importance. The peculiar form of the deposit in and upon many kinds of hairs is a distinguishing mark, and in many it is so general and abundant that an indestructible cast of the hair remains with the cuticle, after maceration or burning of the leaf on which it is found.

This is particularly the case with the large and striking stellate hairs of the Deutzias. In these hairs as well as in many others (as for example: those of *Onosmodium*, *Lithospermum*, *Benthamia* and *Astragalus*), the silica is disposed in apparently granular masses, distributed over the surface of the hair, giving it the appearance of the larger and coarser spicules of some of the Gorgonidæ.

Under a high power these grains have sometimes seemed to me more like irregular truncate cones, or like the deposits of silica or lime which form on a larger scale around the mouths of geysers and hot springs, and I have therefore imagined that perhaps they were actually formations about orifices from the interior of the hairs, though I have never been able to demonstrate, to my own satisfaction, any such opening through them.

Before passing to another division of my subject, I must say a few words about stomata, which also are epidermal structures. As a general rule they are found upon the same parts as the hairs and glands, and in the same relative proportions. That is to say, they abound upon the leaves and homologous parts, and on young and growing stems and branches; and they are found in most abundance on the under side of leaves. Unlike hairs, however, they never appear upon the mid-rib and veins but are always found directly over intercellular spaces, of which they are the means of communicatlon with the external air. Of course they are useless, and therefore exist but as stragglers, if at all, on parts not exposed to the air. They are therefore not usually found on true roots or submerged parts of aquatic plants. Like hairs, their relative number upon the upper and upon the lower side of the leaf depend in great measure upon the natural position of the leaf with reference to the light.

I will now pass to the physiological portion of my subject.

It is not to be doubted that such highly developed and specialized organs as plant-hairs have an important physiological office in the vegetable economy. Neither is it to be supposed that so large a part of the mere bulk of the plant is practically useless or only ornamental. The fact that the hairs of plants constitute a very large proportion of their substance, argues that they are not accidental or merely incidental growths, but that they must be exceedingly important organs to warrant such an expenditure of material and energy as is necessary for their production. We all appreciate the extraordinary quantity of material used to form the seed-hairs which constitute the commercial article, cotton; and all have observed the also lavish use of material made to produce the seed-hairs of the milk-weed and the thistle. These seed-hairs serve a useful purpose in the distribution of the seeds to a distance, thus disseminating the species to which they belong; but aside from this I believe that, in common with other plant-hairs, they serve an important physiological purpose before the seeds upon which they grow attain maturity.

It seems to me that light is thrown upon the office of plant-hairs in general, by what we know of the physiological uses of root-hairs and the tentacular hairs of the insectivorous plants. Such hairs are primarily absorbing organs, taking up for the use of the plant not only nitrogen and nitrogenous compounds, but probably also oxygen.

It is generally agreed that there are but two principal physiological processes going on in the plant, namely, assimilation (the elaboration of organic compounds out of inorganic), and metastasis (the transmutation of one organic compound into another). Assimilation is that process by which carbon-dioxide and water are decomposed and their elements formed into what are known as the carbo-hydrates, of which starch is the most important. In this process oxygen is liberated and exhaled. Assimilation can take place only in the chlorophyll-bearing cells, in the presence of light and a certain degree of heat. The materials produced by this process are the only materials which are suitable for use as food for the protoplasmic basis of life in the plant, which is the seat of growth and reproduction. The process by which these carbo-hydrates are appropriated to the specific purposes of the plant, are transported from one part to another, and transmuted into active, living, propagating and then permanent vegetable tissue, is what is called metastasis. Inorganic substances cannot be directly appropriated by the protoplasm of the plant, except perhaps to a very limited extent in some special cases. Assimilation, therefore, is a somewhat doubtful name for a preparatory process, of which metastasis is the ultimate object. Metastasis is, therefore, really the assimilative process, and corresponds to the process to which the name assimilation is given in animal physiology; while assimilation, so-called in vegetable physiology, is more analagous to the preparatory process of digestion in animals. There is greater analogy between the vegetal process of metastasis and the animal process of assimilation from the fact that oxidation, by some sort of respiration or absorption from without, is an essential part of each.

It has already been stated that what is termed assimilation, takes place only in the chlorophyll-bearing cells in the presence of light and heat. Therefore, fungi, parasitical plants and, generally, plants which are destitute of chlorophyll, are unable to perform the assimilative process. They must therefore obtain for their food ready-made, organic compounds, and are, in this respect, like animals.

Unlike the process of assimilation, metastasis takes place in cells which do not bear chlorophyll, or else in the chlorophyll-cells in the absence of light; and while the assimilative process is promoted by light and warmth, the metastatic process is promoted by darkness and probably by a lower temperature. What aids the one process retards the other; so that the assimilative process is active in the day-time when the metastatic process is checked, and the latter process is active at night when assimilation is checked. Day-time is therefore the period of preparation, and night time the period of growth in plants. In the day-time they take up and decompose the compounds from which the carbohydrates are formed, at the same time exhaling oxygen, and at night they inspire oxygen for the purposes of internal change and growth, at that time exhaling the products of oxidation, which consist mostly of carbon-dioxide. Now this fact is to be particularly noted, that the protoplasm of the plant is its life-bearing element, and that the process of metastasis is a process directly connected with the preservation, augmentation, modification and reproduction of this life-bearing element; while the process called assimilation is almost purely chemical, and has for its result merely the production of appropriate material for the metastatic process.

It has been shown that the rotation of protoplasm in the plant-cell is not aided by light, if, indeed, it does not take place more readily in the dark. It has also been shown that it cannot take place without a supply of oxygen. It is also a familiar fact that the rotation of protoplasm is common in plant-hairs, in which it may be seen under the microscope. A favorite object for this purpose used to be the stinging hair of the nettle, but the cyclosis is easily seen in many other hairs, particularly in the segmented hairs on the stamens of *Tradescantia* and in the leaf-hairs of the pansy or of the holly-hock. The facts I have just referred to serve to connect the hairs with the protoplasmic portion of the plant and, through it, with the process of metastasis.

As there are two essential physiological processes in plant-life, so there are two principal sets of organs for the effecting of these processes, namely, the chlorophyll-cells with their appendages, and the circulatory system with its appendages. The former system is apparently much the simpler, and consists of little besides the chlorophyll-cells themselves (which are parenchymal cells), with the stomata, their means of communication with the external air. But the circulatory system begins in the roots, follows the trunk, branches, stems and petioles, and spreads out in a finely ramified network of veins in the leaf, the latter being merely the extension of the fibro-vascular bundles from the petiole into the leaf.

Circulation in the plant is dependent upon evaporation from its surfaces. The leaves promote evaporation, and the lost moisture is made good mainly by absorption of water through the roots. There are reasons for supposing that the stomata are the chief organs of evaporation, especially in those plants which have a dense and impervious cuticle. But there are also good reasons for believing that the stomata have other offices besides merely facilitating evaporation. There can be but little doubt that they are also the means of communication between the external atmosphere and the internal chlorophyll-bearing cells through which the supply of materials is obtained for the process of assimilation already described. Such a relation between the stomata and the chlorophyll-cells is at once suggested by the fact that the stomata are invariably directly over intercellular cavities ; and it is confirmed by the fact that they open in the presence of light and close in darkness, being ready for duty only at a time when the assimilative process is active. If the function of evaporation were their sole office, one would suppose that they would be most open when evaporation was least active (in the shade), and more closed when evaporation was likely to be too rapid (in the sunlight), acting, in this respect, like the governor on an engine.

While there is much evidence that the stomata are organs of the assimilative process, there is quite as much evidence that they are not connected with the metastatic process. Of this negative evidence we recall at once the fact that the stomata are never found upon the fibro-vascular veins of the leaf. Other negative evidence will suggest itself as the converse of postive evidence which will hereafter be mentioned as showing that the hairs are connected with, and are organs of, the metastatic process.

Several recent observers of plant-hairs have attempted to account for their existence ; but no one, as far as I know, has done so upon purely physiological grounds. To my mind, however, the evidence that hairs are primarily organs of the metastatic process, strengthens with each new fact that comes to my knowledge. This theory is not affected by the fact that not all plants in all stages of their existence are hairy, because, probably no process in vegetable physiology is performed in precisely the same manner, and by exactly the same means throughout the whole kingdom. Nor is the theory weakened because hairs often serve other purposes than strictly physiological ones, for nothing is more common than for an organ, or part, to become modified or specialized for an office for which it was not primarily intended. Thus it is by no means strange if hairs, while essentially organs of the physiological process of metastasis, should be utilized for purposes of protection against cold or dryness, as has been suggested by some of the writers to whom I have alluded. I have no doubt that they are in most instances correct in their inference that great hairiness or wooliness may be a protection against sudden changes of temperature, or a check upon too rapid evaporation. Nevertheless, I cannot find that unusual pubescence is generally associated with a warm, or a cold, or a dry climate, although this last relation is the most plausible. It seems to be a fact, however, that the hairiness of a plant bears some proportion to the general sterility of the region in which the plant grows. In confirmation of this I am informed that, in the sterile regions of our western territories, not only do the more hairy species and genera prevail, but those which are hairy elsewhere are especially so there.

Mr. Charles Darwin is plainly of the opinion that the saprophytic habit of the so-called insectivorous land plants is the result of a struggle against sterility of soil, but not particularly against dryness ; for while these plants usually inhabit sandy or barren regions, they quite as commonly grow in very wet places. Such being the case, it seems altogether natural that we should find a general increase of pubescence in the plants of a desert region ; for what is the cause of a most remarkable specialization in the case of the insectivorous plants, may readily be conceived to be the cause of a less remarkable modification in the general flora of a district. A further fact, strengthening this idea, has also been noticed by Mr. Darwin, in his work on insectivorous plants, viz. : that the high degree of specialization in the glandular hairs of these plants is associated with smallness of the roots, the latter being in most cases barely of sufficient size to collect water from the soil. In some genera, indeed, as, for instance, in *Dionæa*, the plant does not seem to depend upon the soil at all, for this plant may be grown epiphytically upon moist cotton or sponge.

It is well known that roots and foliage-branches are homologous parts, so that in some plants they may easily be made to exchange places and functions, the branches when planted in the soil running to roots, and the roots when turned upwards developing into foliage. It is therefore not astonishing that, in their natural position the roots and their appendages and the leaves and their appendages should maintain a more or less steady equilibrium. When, for any reason, the plant does not find use for the natural root functions, we should expect it to transfer them to the leaf if possible ; and where the supply of oxygen and nitrogen compounds is cut off at the root—as it is in a desert region—it is quite in accordance with analogy that the leaf organs should be unusually developed, for the purpose of increasing the supply of oxygen or of nitrogenous compounds through the leaf. This will be particularly the case when the assimilative process is not active, and when the plant must therefore, rely more upon obtaining organic compounds ready-made than upon making them itself.

Aside from the question of the abundance or scarcity of food, the plant's means of appropriating its food-elements must be in proportion to the requirements of growth. That is to say, other things being equal, a rapidly growing plant, or part of a plant, is more likely to be hairy than is a slowly growing plant or part. On this principle, as I have already mentioned, the newest part of a plant, whether leaf-bud or flower-bud, is usually the most pubescent part.

It is not easy to account for all the differences among genera, as to hairiness or smoothness, but I have no doubt that ultimately it will be ascertained pretty nearly why each different genus is or is not hairy ; for I do not think there can be a doubt that every such difference has a reason, founded in general laws, in the main physiological.

In the insectivorous plants some of the hairs are adapted to a use not strictly physiological, namely, the alluring and capturing of prey. For this reason they have become most developed and modified on the upper instead of the lower side of the leaf. It is not unusual, however, to find organs of every kind which have become specialized for peculiar purposes; and an instance, somewhat in the line of the alluring bait of some of the insectivorous plants, is the change which a simple gland, such as we find on many leaves and petals, is supposed to have undergone, in order to produce the nectary of the flower.

Where hairs have not been modified for unusual purposes, we can see reasons why they should grow most abundantly and luxuriantly on the under side of the leaf. In the first place, the hairs, being organs of the metastatic process, naturally grow, under ordinary circumstances, where that process is best promoted, namely, in the shade, where also, for the same reason, are the veins with which the hairs are connected. But aside from this, it seems to me not merely a fancy that, as the upper side of the leaf is the one where the chlorophyll-cells most naturally abound, it should be free from any organs which would cut off the full supply of light and heat which is necessary to the operation of their functions. Moreover, since the stomata open in the light, and evaporation is hastened by heat, the under side of the leaf seems to be the better place for them, for there they are less liable to unrestrained action which would be disturbing and dangerous to the plant. Besides this, we can see that it is an economical arrangement that hairs and stomata should exist together, chiefly for the reason already referred to, that the hairs probably help to retain moisture and check too rapid evaporation.

After this hasty and necessarily imperfect summary of the more general facts known as to external epidermal organs, I wish now to call attention briefly to some facts concerning analogous internal organs. These are particularly the internal hairs of some water plants, of the genera *Nymphæa* and *Nuphar*.

If we examine with the microscope a section of the leaf, or the petiole, of a plant from either of these genera, we are at once struck by certain abundant, thickened, branching, unicellular structures scattered through the parenchyma and projecting into the intercellular spaces. These structures have long attracted the attention of microscopists, but not until recently have they been distinctly recognized as internal hairs. The standard text-books of the microscope, such as Carpenter's and the Micrographic Dictionary, refer rather doubtfully to the resemblance between these bodies and the stellate external hairs of *Deutzia* and *Alyssum*, but they generally shyly avoid calling them plainly internal hairs. Some writers speak of them as "stellate parenchymal cells;" and on a purchased slide which I own, they are described as "stellate raphides." But out of the confusion and uncertainty which has prevailed with regard to these structures, there has gradually crystallized a clear and definite recognition of the fact that they really are epidermal organs, exactly analogous to the external hairs of terrestrial plants, such as we have been considering.

In the first place, the mere morphology of these structures confirms the idea of their being truly hairs. In their outlines they so closely resemble some of the external hairs with which we are familiar (for instance those of the genus *Arabis*), that their analogy is at once suggested to the observer. They seem, however, to be always unicellular growths, and transverse sections show them to be hollow. Over their surfaces are scattered the grains of silex, so characteristic of other hairs, and made particularly familiar to us by the hairs of the Deutzias. If one wishes a striking demonstration of the mere resemblance of these internal hairs to better known external hairs, he has only to split the petiole of *Nuphar* or *Nymphæa* by tearing, and view it with the binocular as an opaque object. This, of itself, will be convincing to most persons acquainted with the peculiarities of leaf-hairs.

But, aside from configuration and other merely morphological considerations, the mode of distribution of these internal hairs is almost precisely like that of external hairs. If we take a thin section of a leaf of *Nymphæa*, cut parellel to its surface, and examine it as a transparent object (still better if we illuminate it with polarized light), we shall see that these internal hairs, like external ones, are associated with the fibro-vascular system; and toward the margin of the leaf, where the tissues are thin and the veins small, we shall find that the hairs exist only upon the veins and not between them. This is quite in accordance with what we know of the habit of all hairs, as I have already explained.

If we take a transverse section of the leaf of *Nymphæa* or *Nuphar*, cut across the mid-rib, we shall be struck by another fact connecting these internal hairs with the epidermal system. We shall at once notice that from the upper side of the leaf—which is, under common circumstances, the only side exposed to the air, and is consequently the only side possessing a true epidermis—these hairs spring like stumps of trees in an inverted field. From end to end of the section they will be observed planted close together, their pedicels imbedded in, or forming a part of, the epidermal layer, and their branches spreading downward and inward through the underlying parenchymal tissue. This is very marked in stained sections, in which the hairs take a darker color than the surrounding tissues; but in an unstained section, polarized light differentiates the structures quite as well as the elaborate, double-staining process now so commonly employed. It is to be noted that this arrangement of the hairs is confined to the upper or epidermal side of the leaf, and that no similar arrangement is to be seen at any other part. The distribution of the hairs on the interior of the petiole of the water plants is somewhat different from their arrangement on the interior of the leaf, but it is closely analogous to the arrangement of hairs upon the exterior of the petiole of land-plants.

I have referred to the fact that these internal hairs are good objects upon which to use polarized light; and this is a point of no small importance in the argument for their being actually hairs. To any one acquainted with the behavior of vegetable tissues with the polariscope, particularly of vegetable hairs, the manner in which these internal structures of the Nymphæaceæ are affected by polarized light is strong confirmation of their claim to be regarded as epidermal organs and true hairs. The way in which they take different colors in the process of double staining, will be another affirmative argument with those familiar with that process and its effects. Suffice it to say in this connection, that these internal hairs behave in precisely the way, and take exactly the colors, that external hairs do.

That structures physiologically referable to the epidermal system should be found growing in the midst of the parenchymal system, is not altogether anomalous, for sections of the leaf and petal of *Magnolia grandiflora* reveal an abundance of thickened, irregular, unicellular structures scattered through the parenchyma, which, both in their appearance and in their mode of distribution, at once suggest some sort of similarity to the internal hairs of *Nymphæa* and *Nuphar;* but which, in my judgement, are parts of the glandular system of the Magnolia. Indeed, any true sunken gland may be regarded as an internal epidermal organ.

Plants which do not live either entirely in the water or entirely out of it may naturally be expected to occupy, so far as their organization is concerned, a position intermediate between submerged plants and aerial plants. Such is the case with the Nymphæaceæ. While not relinquishing their dependence upon, and their connection with, the external atmosphere, they nevertheless provide against partial submergence, by an increase of their capacity for internal interchange of the gases necessary for their life and growth. In other words the amount of external surface exposed to the atmosphere being largely curtailed, by reason of their partial submergence, this loss is compensated for by a great increase in the amount of internal surface exposed to the air and gases contained in the intercellular spaces. By this enlargement of the intercellular spaces the inside of the plant becomes (if I may be allowed the paradox) to some extent, for physiological purposes another outside; and the practical effect is the same as if there were less intercellular space, and more surface exposed to the outer atmosphere. To the same extent as the inside becomes practically a part of the outside, by reason of its exposure to surrounding air and gases, that part of the outside which is submerged becomes practically part of the inside, by reason of its exposure to the surrounding fluid.

In plants existing under such peculiar circumstances, we need not be surprised to find organs and tissues which, in strictly terrestrial plants, are external, becoming internal. And so there is no *à priori* reason against the existence of internal hairs, or even of a whole internal epidermal system, in the Nymphæaceæ. But we have no warrant for looking for internal hairs in all partially submerged, or wholly aquatic, plants, any more than we have for expecting to find external hairs upon all terrestrial or aerial plants. As a matter of fact, hairs do not exist upon many land-plants which seem to grow under the same circumstances and surroundings as others, upon which hairs are found; and so, while *Nymphæa* and *Nuphar* are internally pubescent, *Nelubium* and *Bracenia* are internally glabrous. It is no easier to account for this difference in land-plants than it is in water-plants; but in both cases it is doubtless caused by some fundamental, physiological difference at present unknown.

That the great enlargement of the intercellular spaces in submerged, or partly submerged, plants, is for the purpose of facilitating the internal interchange of gases which, in plants growing upon the land, would take place externally, is no new theory of my own. Sachs, in his "Botanical Text-Book," says:—

"A submerged water-plant, for example, which contains chlorophyll, absorbs carbon dioxide from without, under the influence of sunlight; and at least a portion of the disengaged oxygen collects in the cavities. When it becomes dark this process ceases; the collected oxygen is now absorbed by the fluids of the tissue, and gradually transformed into carbon dioxide, which can again diffuse back into the cavities, but partially also through the layers of tissue into the surrounding water."

In the light of these facts we can perceive how the interior of a water-plant may become of more importance to it than the exterior, for most physiological purposes, and under these circumstances it is not strange that we find such important organs of the metastatic process as the hairs, transferred from the exterior to the interior, where the amount of surface exposed to the interchanging gases is many times greater than that exposed to the external atmosphere.