ART. XXV.—*The root-structure of North American terrestrial Orchideæ;* by THEO. HOLM. (With figures in the text.)

FEW orders have offered a larger number of interesting data in the various phases of the life-history of plants than the *Orchideæ*. By their manifold structures, readily perceivable among their various biological types, they have for years attracted considerable attention and furnished ample material to writers on morphological and anatomical botany. It is quite natural that the epiphytic species have received a more general treatment than the terrestrial, on account of their unquestionable prominence in floral and vegetative characters, besides that their cultivation being less difficult has made them more accessible to study than the others. Among the terrestrial species very few have been studied from a general point of view except old-world species, but several of these have, nevertheless, served as the very basis of such magnificent contributions to science as those of Irmisch. While, thus, our native, terrestrial *Orchideæ* are very little known from a morphological and anatomical point of view, the following notes on their root-structure are offered as a small contribution to the knowledge of these interesting plants, with the intention to add some further observations in a subsequent paper, which we have made upon the other organs.

As a general result of these observations we might state here, that it seems to be a rule that a tuberous rhizome is only provided with slender roots as is the case with *Arethusa*, *Calypso*, *Bletia*, *Tipularia*, *Aplectrum*, etc., while species with slender rhizome may possess tuberous roots, as for instance: *Orchis spectabilis*, *Platanthera*, *Spiranthes*, etc., or the roots may be equally slender, as in *Cypripedium*, *Goodyera* and certain species of *Pogonia: verticillata*, *ophioglossoides* and *divaricata*.—We might, also, call attention to the fact, that the development of such varied structures of roots and rhizomes does not seem to be dependent upon any special nature of environment; on the contrary, species with tuberous rhizomes may occur in open bogs as well as in deep, shaded woods; and species with tuberous or slender roots may be found in bogs, ravines, in dry fields or in clearings in thickets. In this particular respect the plants themselves seem to possess a very pronounced individuality, and are difficult to classify as meso-, hydro- or xero-phytes. It appears even to be rather uncertain whether some of these species are to be considered as auto-phytes or hemisapro-phytes.—And when we consider the general structure of the roots alone, it seems quite

impossible to offer any satisfactory explanation as to certain facts, for instance, the presence of a velamen in *Tipularia discolor*, and its absence in *Aplectrum*, although the nature of the surroundings, the substrate even, is the same in both, and they both are terrestrial. In *Bletia verecunda*, on the other hand, the development of a similar velamen may be explained as an inherited character, since other species of the genus are epiphytic. A similar approach to the epiphytic root-type as demonstrated by certain species of *Spiranthes* is, also, very puzzling, inasmuch as this genus does not, otherwise, exhibit any analogies in common with epiphytes.

From these data, it may be readily appreciated that the *Orchideæ* are not to be classified in anything like natural sequence based upon root-structure alone, and we have thought, therefore, that it would be the most convenient to treat the different types of roots by themselves, and regardless of the natural affinities of the genera or species in question. In this way a general idea of the root-structure may be obtained with less difficulty.

The following types may be distinguished as characteristic of the terrestrial species:

A. Roots slender with the leptome and hadrome located in one central-cylinder.

B. Roots tuberous with the leptome and hadrome located in one central-cylinder.

C. Roots tuberous with several cylinders of leptome and hadrome.

Of these types the first, A, represents several cases of deviation from the ordinary root-structure by the presence of a velamen for instance (*Tipularia*, *Bletia*), by a peculiar striate thickening of cortex (*Liparis*), and by the development of a true pith (*Calypso*, *Goodyera*, *Habenaria*, etc.). The second type, B, is especially characteristic by reason of its large dimensions, due to numerous layers of cells in cortex and pith, while the third, C, as already indicated, possesses several mestome-cylinders.

Type A.

Cypripedium acaule Ait., *C. pubescens* Willd., *C. guttatum* Swtz., *C. montanum* Dougl., *C. fasciculatum* Kellogg, *C. Californicum* Gray and *C. arietinum* R. Br.

In the genus *Cypripedium* the root-structure comes nearest that of a normal root and may be described as follows: The epidermis is thin-walled in all the species enumerated above, with the exception of *C. guttatum*, in which the outer cell-wall is slightly thickened; root-hairs are usually abundant. A thin-walled hypoderm of one layer is, also, noticeable, but is

moderately thickened in *C. guttatum*. The cortical parenchyma consists of from 6 to 8 strata with large deposits of starch; it is quite compact, but thin-walled, except in *C. pubescens*, where the cell-walls are thickened and porose. Endodermis is mostly thickened as an U-endodermis outside the leptome, but it is otherwise thin-walled, and the following deviations may be mentioned. In *C. acaule*, *guttatum* and *arietinum* 3 to 4 thick-walled cells were observed outside the leptome, while 6 in *C. Californicum;* in *C. pubescens* and *C. montanum* 2 to 4 cells were thickened like an O-endodermis outside the leptome, while in *C. fasciculatum* the entire endodermis was found to be thin-walled throughout. The pericambium is only represented by a single continuous layer in all the species; it is thin-walled except in *C. arietinum*. The rays of the hadrome are very broad and meet in the center; they average from 5 to 10, 8 to 10 being the characteristic of *C. montanum;* a thick-walled pith forms a small central group in *C. Californicum*, but not in the others. The leptome is well developed in large groups alternating with the rays of the hadrome.

None of the roots were found to be contractile, and hyphæ were noticed in: *C. pubescens* (epidermis, hypoderm and cortex), *C. fasciculatum* (cortex) and *C. guttatum* (endodermis and pericambium).

Epipactis gigantea Dougl.

Epidermis, hypoderm and cortex are all thin-walled, and much starch is deposited in the cortical parenchyma. The endodermis is thin-walled throughout with the Casparyan spots plainly visible and with contents of starch; the pericambium forms a closed ring around the leptome and hadrome; it consists of only one layer, the cells of which are prominently thickened outside the leptome, but otherwise thin-walled. Five broad rays of hadrome extend to the center of the cylinder and alternate with large, roundish groups of leptome. No hyphæ were observed.

Listera cordata R. Br. and *L. australis* Lindl.

The structure of the roots of these two species is almost identical, and the difference depends merely upon the relative development of hairs, which are very numerous and long in the former species, but quite scarce in the latter; moreover, the leptome constitutes groups of quite large dimensions in *L. cordata*, but not in the other species; otherwise the structure is identical. Epidermis and hypoderm are thin-walled, and the cortex which occupies the greater portion of the root is composed of about 5 layers, the cells of which are very large, thin-walled and filled with starch; the intercellular spaces are

narrow. Endodermis is moderately thickened all around, while the pericambium is thin-walled and continuous in *L. cordata.* Five narrow rays of hadrome meet in the center with five relatively wide vessels, and alternate with roundish groups of leptome; the conjunctive tissue is thin-walled and is only to be observed between the vessels, but not in the center of the cylinder. Hyphæ were observed in epidermis, hypoderm and cortex of *L. cordata*, but not in *L. australis.*

Pogonia ophioglossoides Nutt., *P. verticillata* Nutt. and *P. divaricata* R. Br.*

Epidermis is thin-walled and densely covered with hairs in *P. ophioglossoides* and *divaricata*, but less so in the third species. The hypoderm is thin-walled in *P. ophioglossoides*, slightly thickened in the others. The cortex is composed of 6 to 9 layers of thin-walled cells; it is quite open in *P. ophioglossoides*, but very compact in the other species. Starch was only found in *P. divaricata.* Endodermis is thin-walled throughout in *P. ophioglossoides* and *P. divaricata*, but in *P. verticillata* there is one thick-walled cell outside each group of leptome. The thin-walled pericambium is continuous in *P. ophioglossoides*, but is irregularly interrupted by the protohadrome vessels in the two other species. The leptome represents quite large and roundish groups alternating with narrow rays of hadrome; 5 rays were observed in *P. ophioglossoides*, 6 in *P. divaricata* and 8 in the third species; the hadrome extends to the center of the cylinder in *P. ophioglossoides*, but not in the other species. Hyphæ were found in the hypoderm and cortex of all three species.

Calopogon pulchellus R. Br., *C. multiflorus* Lindl. and *C. parviflorus* Lindl.

The root-structure is very uniform in these species and resembles that of *Pogonia*, especially *P. ophioglossoides.* Epidermis and hypoderm are thin-walled in all three species, and the cortex, which, also, is thin-walled, consists of about 8 layers with narrow intercellular spaces; no starch was observed in the cortex. The endodermis is thin-walled throughout, with the spots plainly visible. In the central-cylinder we find a thin-walled pericambium in the two first species, but one moderately thickened in *C. parviflorus;* it is continuous in *C. pulchellus*, but we were unable to trace the exact location of the protohadrome vessels in the other species, whether these had broken through the pericambium or not. Five, and quite broad, hadromatic rays were observed in *C. pulchellus* and *C. parviflorus*, but only three in *C. multiflorus;* the innermost vessels are relatively wide and border on a small, but very distinct, cen-

* Compare this Journal, vol. ix, 1900, p. 13.

tral group of slightly thickened parenchyma. The leptome occurs as small, roundish groups in transverse section. Hyphæ were found in the cortex of *C. multiflorus* and *C. pulchellus*, but none in the third species.

In the following genera of this same type the roots are quite slender, but possess in contradistinction to those described in the preceding, a well developed central parenchyma, which evidently represents a true pith, homologous with the pith of the stem.

Habenaria repens Nutt.

This species is a native of very damp places, and when growing in water the very long roots produce root-shoots: A thin-walled epidermis with few hairs and a hypoderm surround a cortex of about 20 layers of thin-walled cells, of which the outermost 4 constitute a compact and persisting tissue, while the interior 16 are traversed by numerous lacunes from the very wide intercellular spaces; only a little starch, but many bundles of raphides were observed in the cortex, besides hyphæ in the peripheral strata. The cortical parenchyma is, thus, very open, and in several roots, in the entire length of these, a well defined duct was furthermore observed, surrounded by a sheath of very small, thin-walled cells; neither liquid or solid contents were observed in this duct, and its function may evidently be for osmotic exchange of gases.

The endodermis and the continuous pericambium are both thin-walled. In regard to the hadrome and leptome, the former does not occur in rays, but merely as small groups, from 6 to 15, each consisting of a few, 2 to 5, mostly wide vessels, which to a more or less extent alternate with the equally small groups of leptome. The arrangement of the hadrome in proportion to the leptome is somewhat irregular, and we observed several cases where the leptome was really located in front of the hadrome, thus imitating the radial position of these same elements in the stem; in other cases the vessels were on each side surrounded by a group of leptome with the two proto-leptome cells very distinct (fig. 1), as in mestome-bundles of the hadrocentric type, and this position was frequently observed in *H. repens*. The larger portion of the central cylinder consists of a thin-walled pith with deposits of starch.

Arethusa bulbosa L.

The epidermis is thin-walled and densely covered with long hairs; there is, also, an hypoderm, but not easily distinguishable from the cortex. The latter consists of about 6 compact layers with many hyphæ, but without starch. Endodermis and the continuous pericambium are both thin-walled and surround

6 short, but broad groups of rather narrow vessels, alternating with a corresponding number of small groups of leptome, while a pith occupies the greater inner portion of the central-cylinder.

Calypso borealis Salisb.

The structure of the root is almost identical with that of the preceding, and the only differences observed were as follows: the hypoderm is very distinct and the cell-walls are slightly thickened; the cortical parenchyma is a little broader and quite open, the intercellular spaces being relatively wide; the hadrome occurs only as small, 3 to 6, groups of vessels, alternating with the leptome and separated from the center by a large mass of thin-walled pith.

Goodyera pubescens R. Br., *repens* R. Br., *Menziesii* Lindl. and *tesselatum* Lodd.

In respect to the root-structure these species resemble each other very much, and we find in these the same delicate structure of the various tissues, as described above as characteristic of *Arethusa* and *Calypso*. The roots are very hairy, the epidermis, the hypoderm, the cortex, the endodermis and the continuous pericambium are all thin-walled; of these, the cortex consists of about 6 layers in *G. repens* and *tesselatum*, of 8 in *G. pubescens*, and of about 12 in *G. Menziesii;* it is quite compact in all the species except in *G. tesselatum*, in which the intercellular spaces are much wider than in the other species. The hadrome and leptome constitute small groups, when viewed in transverse sections, the former with 4 to 8 vessels in each group, widely separated from the center of the cylinder by a large, starch-bearing and thin-walled pith. The number of hadromatic groups is somewhat variable within the species examined; thus 4 were observed to be characteristic of *G. repens*, 5 of *G. tesselatum* and 6 of the other species. No hyphæ were found in the internal tissues of *G. repens* or *G. tesselatum*, but in the cortex of the others.

Chlorœa Austinœ Gray.*

Although the roots of this plant are relatively strong, much more so than in any of the other *Orchideœ* described above, the structure does not reveal any very pronounced mechanical

* The statement by Mr. MacDougal (Bull. Torrey Club 26: 528, 1899) that "this plant is to be added to the list of chlorophylless plants furnished with stomata" is not correct, since we have observed the presence of chlorophyll-grains in the ovary; the guard-cells of the stomata as well as the adjoining epidermis-cells are well supplied with chlorophyll. The description and the figures furnished by this author (l. c.) are altogether very inexact.

equipment. The only tissues which exhibit some thickening are the endodermis and the large, central parenchyma; of these the former is, however, only thick-walled just outside the leptome, and only moderately so. The pith is not thickened very much either, but it occupies such a prominent part, that it necessarily contributes a great deal to the toughness of the root. But the other tissues are thin-walled, and the cortex is composed of 15 compact layers, densely filled with starch and some hyphæ. The pericambium is continuous and surrounds 6 broad rays of hadrome with rather narrow vessels, arranged very regularly in alternation with the large groups of leptome, and border on the very prominent, central pith.

Aplectrum hyemale Nutt.

The densely hairy epidermis, the hypoderm and cortex are all thin-walled, and the last of these consists of about 9 layers with narrow intercellular spaces; no starch or hyphæ were observed, but bundles of raphides. The endodermis and the continuous pericambium are, also, thin-walled and surround 9 broad rays of hadrome, alternating with large, roundish groups of leptome with a central mass of thin-walled pith.

Liparis liliifolia Rich.

The very slender roots show a very feeble structure since all the tissues from epidermis to pith are of a very delicate texture. The epidermis bears many long hairs; the hypoderm is well differentiated from epidermis and cortex by the cells being somewhat stretched radially and almost regularly pentagonal. The cortex consists of about 8 layers and contains a few hyphæ, but no starch; it seems characteristic of certain species of the genus that some of the cells of the cortex exhibit the same spiral thickening of the wall as is well known from the roots of epiphytic genera, a fact that has already been mentioned by Irmisch.* The endodermis is very thin-walled and shows the spots very plainly; the pericambium is continuous and surrounds 12 small groups of hadrome, each with a few vessels, and a corresponding number of small groups of leptome, while a large pith occupies the inner portion of the central-cylinder.

Tipularia discolor Nutt.

As stated above, the roots of this plant show the remarkable structure of possessing a velamen of 3 to 4 layers inside a thin-walled, very hairy epidermis. However this velamen differs from that of the epiphytic *Orchideæ* by lacking the character-

* Beiträge zur Biologie und Morphologie der Orchideen, Leipzig, 1853, p. 34.

istic spiral or simply striate thickening of the cell-walls; otherwise the structure is identical. There, is, furthermore, an exodermis of exactly the same structure as we know from the epiphytic genera. The cortical parenchyma is thin-walled and consists of about 8 layers of roundish cells with narrow intercellular spaces; many hyphæ, but no starch, was observed in this tissue. The endodermis and the continuous pericambium are both thin-walled and surround 5 short rays of hadrome, alternating with 5 small groups of leptome; a pith occupies the inner portion of the central-cylinder.

Bletia verecunda Sw.

In several respects the root-structure of *Bletia* agrees with that of *Tipularia*, but some, and indeed quite important, deviations were noticed. These consist in the more typical development of velamen, the cell-walls of which exhibit the characteristic fine and spiral thickening peculiar to this tissue; moreover by the presence of a double pericambium, which is moderately thickened and to the same extent as the hadrome, thus the position of the proto-hadrome vessels in proportion to the pericambium could not be made out satisfactorily. The hadrome forms 8 short and broad rays alternating with large, roundish groups of leptome, inside of which there is a large, thin-walled pith with intercellular spaces of quite considerable width.

These roots, described above, belong to the first type, all being relatively slender and possessing only one, central-cylinder. In several respects they agree with the second type, in which, however, the dimensions of the roots have increased to such an extent as to deserve the term "tuberous" on account of the much broader zones of the cortex and pith, besides by the larger number of rays or better "groups" of hadrome and leptome.

Type B.

Spiranthes gracilis Big., *S. simplex* Gray, *S. præcox* Wats., *S. Romanzoffiana* Cham., *S. cernua* Rich., *S. cinnabarina* Hemsl. and *S. Asagræi* Schaff.

Even when the roots are quite numerous, as in the last two species, they, nevertheless, retain the same swollen aspect as when they are but few in number or single, as in *S. simplex*. The internal structure is, also, very uniform in these species, and not very different from those described above, but pertaining to other genera.

Common to these species of *Spiranthes* is a thin-walled epidermis with many hairs, besides a hypoderm of one layer, the cells of which are smaller than those of the adjoining cortex.

And as already described by Irmisch (l. c.) as characteristic of the European *S. autumnalis* Rich., the cells of epidermis show the same spiral thickening as we find in the velamen of the epiphytic genera, besides that a similar thickening of the cell-wall is, also, to be observed in the hypoderm of *S. cinnabarina* and *Asagræi*. The cortex is thin-walled and the cells of the innermost layers are very often stretched radially; the number of layers varies somewhat, but is usually about 15, and the contents consist mainly of starch, except in the last two species, where only hyphæ were observed; it seems altogether as if the function of these fleshy roots of *Spiranthes* is to store starch and not water, although the nature of the habitat might suggest that water-reservoirs would be needed. In *S. simplex* and *S. præcox* no hyphæ were observed in any of the tissues, but in the other species the roots proved to be real *mycorhizæ*. As to the innermost layer of the cortex, the endodermis, this seems to be invariably thin-walled in the species examined and shows the Casparyan spots very plainly. The pericambium is represented by only one layer; it is very irregularly interrupted by the proto-hadrome vessels in *S. gracilis*, *S. simplex* and *S. Romanzoffiana*, but in certain roots of the last species it occurred, also, as a continuous ring, the proto-hadrome being located inside. In *S. præcox* the pericambium was found to be continuous near the base of the root, but interrupted near the apex of same. The rays of the hadrome, from 12 to about 20, are very short in all the species and contain but a few vessels, alternating with similarly very small groups of leptome, while the greater portion of the central-cylinder is occupied by a large mass of thin-walled parenchyma, a true pith.

Type C.

The roots of this type are more or less tuberous and contain several cylinders of leptome and hadrome.

Orchis spectabilis L.

If we examine the tuberous root below the hibernating bud, we notice the following structure. Epidermis is thin-walled and there are many root-hairs. Underneath the epidermis is a thin-walled cortex of about 8 layers containing starch and hyphæ, and which borders on 2 mestome-cylinders separated from each other by a few layers of parenchyma, which shows the same structure and contents (starch) as the peripheral cortex. Each mestome-cylinder is surrounded by a thin-walled endodermis, inside of which is a pericambium, which is broken by the proto-hadrome vessels in several places. The hadrome constitutes about 12 irregular and very short rays, which alter-

nate with a corresponding number of leptomatic groups, while a broad pith occupies the inner portion of the cylinder.

The same structure is to be observed in the slender roots of the same rhizome, with the only exception that these contain only one, central mestome-cylinder, the elements of which correspond well with those of the tuberous root, there being about 15 short, hadromatic rays and small groups of leptome surrounding a large, central pith.

Platanthera.

In North America the genus is exceedingly well represented, and occurs with several very distinct types, distinct not only in respect to their flowers, but also in regard to their vegetative organs. The slender, creeping rhizome of *P. rotundifolia* Lindl. is provided with several slender roots, the structure of which is so near that of *P. obtusata* Lindl., that they may be treated together. But in all the other species of the genus examined, the roots, especially the one beneath the hibernating bud, are more or less tuberous, and exhibit a structure that is nearly identical with that of the other secondary, but more slender, roots of the same rhizome.

P. rotundifolia Lindl. and *P. obtusata* Lindl.

Characteristic of the roots of these species is the sparingly hairy epidermis and the lack of any well defined hypoderm. The cortex is thin-walled in both, quite compact in *P. obtusata*, but rather open and not so broad in the other. Large deposits of starch besides hyphæ were noticed in *P. obtusata*, but only hyphæ in *P. rotundifolia*. Two mestome-cylinders of equal diameter are imbedded in the cortex near the center of the root in *P. obtusata*, while there are two large and one much smaller in the other. These mestome-cylinders are, thus, separated from each other by some strata of parenchyma, which may be properly defined as pertaining to the cortex, with which it agrees in regard to structure. Each of these mestome-cylinders has a thin-walled endodermis and pericambium, the latter being continuous in *P. obtusata*. The rays of hadrome (3 in *P. obtusata*, 1 to 5 in *P. rotundifolia*) are very short and consist of but a few vessels, which, together with small groups of leptome, border inward on a thin-walled pith, which is very prominent in *P. rotundifolia*, but rather inconspicuous in the other species.

P. orbiculata (Torr.) and *P. Hookerii* (Torr.).

Habitually these species are very much alike and very distinct from the other North American species of the genus; their root-structure is somewhat different. This difference,

however, depends merely upon the number and relative size of the mestome-cylinders, there being 4, 2 large and 2 small, in *P. orbiculata*, but 8, and all very small, in the other. Besides this variation as to size, their arrangement is, also, quite distinct, since they are located in one ring in *P. orbiculata*, but in two in the other species. Otherwise the structure is identical; the epidermis, hypoderm, cortex, endodermis and pericambium are all thin-walled, and deposits of starch besides raphides were observed in the cortex of *P. orbiculata*, hyphæ, on the other hand, in *P. Hookerii*. Moreover there are noticed 15 short rays of hadrome in the large cylinders of *P. orbiculata*, but only 5 in those of *P. Hookerii*. A central pith was observed in each of these mestome-cylinders and of both species.

The more slender roots show the same structure as the tuberous, described above, but they contain a correspondingly small number of mestome-cylinders, viz: 3 to 4 in *P. Hookerii*, and only 2 in *P. orbiculata*.

In the remaining species of *Platanthera*, which we have examined: *P. dilatata* (Gray), *hyperborea* (Lindl.), *ciliaris* (R. Br.), *psychodes* (Gray), *cristata* (R. Br.) and *tridentata* (Hook.), the roots show an almost identical structure, since the principal difference observable mainly consists in their relative size, their length, thickness and corresponding number of mestome-cylinders, characters of no great importance when we bear in mind the fact, that the tuberous development of such roots is extremely variable and often depending upon certain conditions of the substrate or upon the individual strength of the specimen.

In beginning with the tuberous roots, the epidermis is quite hairy in some species, but merely papillose in others, for instance *P. ciliaris* and *P. psychodes;* this covering with hairs is especially well marked in specimens from *Sphagnum*-bogs. A hypoderm of a single layer is generally present, but seems to lack *P. dilatata*. The cortex is always thin-walled and contains starch, but the number of layers is very variable even in specimens of the same species; hyphæ were observed in all the species except *P. ciliaris*.

The innermost portion of the root is occupied by a large parenchymatic tissue, which, also, contains starch and which is hardly to be distinguished from the cortex; sphærocrystals were observed in great abundance in *P. ciliaris* and *cristata*. The mestome-cylinders occur, sometimes, in several more or less concentric rings, but are mostly somewhat irregularly scattered, especially when their number is very large, as in the thickest roots of *P. ciliaris*. Their number and relative development is variable, but they contain usually from 1 to 5

rays of hadrome with a corresponding number of leptome-groups (fig. 4). The endodermis and pericambium (End. and P. in fig. 4) are constantly thin-walled, and the latter was found to be continuous in some, but interrupted in others of these small mestome-cylinders within the same tuberous root. A very small, central pith was observed in *P. ciliaris* and *cristata*, but not in the others.

If we compare this structure of the tuberous with the slender roots of these same species, there seems to be no other difference than there being a much smaller number of mestome-cylinders in the latter.

Of the three types of roots observable in our terrestrial *Orchideæ*, the third category emphasizes those in which several mestome-cylinders are present instead of but one, and this peculiarity may be briefly described in connection with the anatomical data, mentioned above. The fact that these tuberous roots contain several, isolated cylinders provided with a special endodermis and pericambium, has given rise to various views regarding their morphological identity: whether the "tubers," as they are frequently called, might represent 1) the basal, swollen part of the bud-axis, 2) a single root, 3) a concrescence of several roots or 4) a concrescence of a stem-portion with leaves and roots. Of these the most generally accepted theory is the one which explains the origin of the tuber as being a concrescence of several roots, very ably discussed by Van Tieghem and others.

But the definition tending to explain the tuber as being the result of a concrescence of a stem-portion with leaves and roots, as proposed by Germain de St. Pierre,* has not been approved by others. Nevertheless, as will be shown in the following pages, this definition does not only seem to be well founded, but is, indeed, the only conceivable one, as far as concerns the tuberous body beneath the hibernating bud in North American *Ophrydeæ;* we may illustrate this by the rhizome of *Platanthera dilatata* (fig. 2). The rhizome of this species is relatively slender and the hibernating bud is prominently removed from the mother shoot by the descending stolon (*St.* in fig. 2); the bud itself (*b*) appears as if it were lateral, since the stolon gradually passes over into the long, tuberous body (*r*) underneath the bud, the so-called "tuber" of most authors. The bud, however, is terminal and its apparently lateral position is due to the growth of the stolon, the direction of which is neither horizontal nor vertical, but simply descending. As may be seen from the figure the basal region of the bud with its rudimentary leaves and young roots is located on the upper, the dorsal, face of the stolon,

* Bull. Soc. Bot. de France, vol. 2, p. 659, 1855.

between the lines 4 and 10. Underneath or better "behind" the bud, as the figure shows, is a cylindrical body between the lines 4 and 10, which cannot possibly be defined as representing a stem (stolon) or a root alone, but appears to be a concrescence of both; the result of our anatomical investigation is in favor of this explanation.

In our figure 2, the dotted lines indicate the places where the most important sections have been laid, and the general structure of the rhizome may be briefly described as follows: At its very base (*st.*) the stolon exhibits a structure like that of a typical rhizome with a distinct central-cylinder, surrounded by an endodermis, and with all the minor characters of a stem-portion. But if we examine a section of this same stolon taken a little further down, by the line 2 for instance, the structure is somewhat different, since we observe there two additional, but very small, mestome-cylinders, which are located underneath the central-cylinder; each of these two mestome-cylinders possess an endodermis and a pericambium (End. and P. in fig. 3) and they represent two roots or at least two primordia of such. By continuing our examination of the same rhizome, we observe in section 3 not less than five small mestome-cylinders besides the central, of exactly the same structure as the two described above, and these are very regularly arranged in an arch which is parallel with the lower face of the stolon. At the same time the epidermal structure has become changed, thus the cells on the lower face of the stolon are more or less extended into papillæ and have attained a darker color in contrast to the epidermis of the upper face, which has retained the typical structure of a stem-epidermis. In other words, the stolon has started to become dorsiventral with the development of roots on its ventral face, accompanied by the characteristic epidermal structure.

In following the structure further down to section 4, the large cylinder, formerly central, has become moved nearer the dorsal face of the stolon, and the number of small mestome-cylinders has increased to ten, arranged in two arches parallel with and located near the ventral face. The distinction in regard to the epidermal structure is still more pronounced in this section, and the dorsal epidermis occupies a zone that is much narrower than the ventral. A gradual increase in the number of mestome-cylinders takes place further down, and thirteen were noticed in the sections taken by the lines 5 and 6; furthermore, by 6, the large mestome-cylinder of the stolon is not only still nearer the dorsal face than we observed before, but its pith has become reduced quite considerably in width. And in regard to the bud, the outermost leaf shows here (at 6) a distinct swelling, caused by a cavity at its base. The broad-

est part of the stolon (by 7) contains the bud, and shows, besides, the thirteen small mestome-cylinders, already observed in the section 5, arranged in two arches parallel with the ventral face of the stolon, and with the points of the arches meeting near the central-cylinder of the bud-axis. The large mestome-cylinder is still visible at the line 8 and a little below, but disappears at 9; from here the small cylinders have increased to seventeen, most of which are arranged near the periphery with a few scattered nearer the center. These peripheral mestome-cylinders are quite small and show the same structure as described above; the interior are somewhat larger, but show, nevertheless, an identical structure.

If we now dissect the part of the rhizome located by the line 11, we perceive the structure that has been described so often as characteristic of the "tubers" of *Ophrydeæ:* a large number (23 in this case) of mestome-cylinders, each with a special endodermis and pericambium, and arranged, but not very regularly, in two zones; the distinction between the two epidermal layers (the dorsal and the ventral) has vanished, and the brownish, conical and tuberous body is now covered all around by papillæ and very short root-hairs.

It would thus appear as if at least the upper portion of the tuberous body of the rhizome of *Platanthera dilatata* and the other North American *Ophrydeæ*, which we have examined, is composed of elements pertaining to a stolon, a bud and some roots, instead of being simply a root, a concrescence of several roots or finally a swollen bud-axis. But in offering our support to this explanation, pronounced so many years ago by the French botanist, we are well aware of the difficulty which confronts any investigator who deals with organs that remain in their primordial stage and which are not known to occur otherwise, as the supposed secondary roots of *Ophrydeæ.*

If we had only succeeded in detecting some distinctions in the cortical parenchyma of the stolon, when the supposed roots make their first appearance, so as to be enabled to discriminate between the cortex of the stolon and that of the roots, then there would have been more substantial proof in explaining this organ as a concrescence of roots and stem. But the only distinction which we have noticed depends upon the variation expressed in the epidermal structure, the constant dorsiventrality of the stolon from the first appearance of the secondary roots, and the structure of the small mestome-cylinders being identical with more slender roots of the same species. Of course the word "concrescence" is somewhat misapplied in this particular instance, since these secondary roots have never been observed to be free, not even at the youngest stage of the stolon or of the bud. But otherwise our definition of the

"tuberous body" may from a morphological viewpoint be justifiable, when we compare the rhizome, and especially the arrangement of the roots, with that of other terrestrial *Orchideæ* in which all the roots are free, slender and with only one central-cylinder. In *Arethusa*, for instance, the disposition of the roots is such that if they were united or grown together, they would exhibit exactly the same structure as we have shown being the characteristic of the lower portion of the "tuber" in the *Ophrydeæ*. But the habit of these plants is too distinct to allow us even to imagine ourselves, that such union of the roots in *Arethusa* might be possible.

Summary.

1. A velamen and exodermis is developed in the terrestrial *Tipularia discolor* and *Bletia verecunda*.

2. Some cells of the cortical parenchyma in *Liparis liliifolia* show the same spiral thickening as is known from the epiphytic genera.

3. A similar spiral thickening was observed in the epidermis and hypoderm of several species of *Spiranthes*.

4. The pericambium is composed of two layers in *Bletia verecunda*.

5. The pericambium was observed to be continuous in a number of species pertaining to different genera.

6. The pericambium was observed to be continuous or interrupted in the same root of *Orchis*, *Pogonia verticillata*, various species of *Spiranthes*, etc.

7. Sphærocrystals abound in the inner parenchyma of several species of *Platanthera*.

8. All the roots of *Epidendreæ*, *Neottieæ* and *Cypripedieæ* examined possess only one central-cylinder.

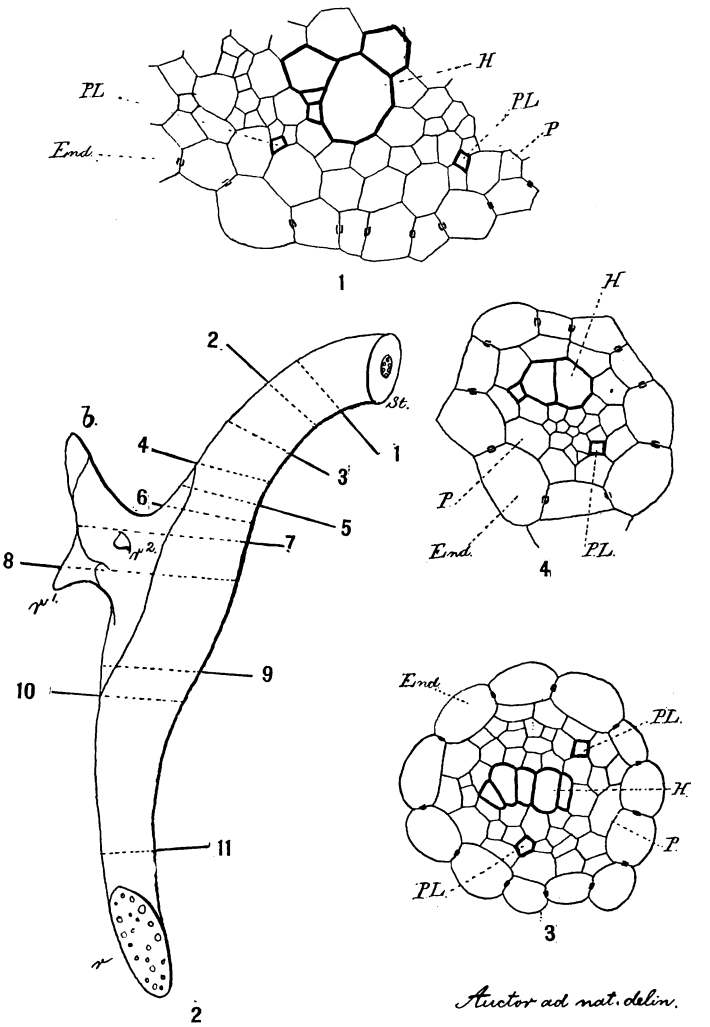
9. A true pith and, sometimes, of quite considerable width was observed in *Tipularia*, *Arethusa*, *Calypso*, *Spiranthes*, *Chlorœa*, *Goodyera*, *Habenaria*, *Aplectrum*, *Bletia*, *Liparis*, *Calopogon* and *Cypripedium Californicum*.

10. The cortical parenchyma is traversed by wide lacunes and by a special duct in *Habenaria repens*.

11. The upper portion of the so-called "tuber" of the *Ophrydeæ* examined consists of elements pertaining to a stolon, a bud and some roots; the lower part, on the contrary, of roots alone.

12. The roots of our terrestrial *Orchideæ* very often represent *mycorhizæ*, but not all the roots of the same species, nor of the same specimen.

Brookland, D. C., May, 1904.



EXPLANATION OF FIGURES.

FIGURE 1.—Transverse section of the root of *Habenaria repens*, showing a part of the central-cylinder; *End.* = endodermis; *P.* = pericambium; *P. L.* = proto-leptome; *H* = hadrome. × 320.

FIGURE 2.—Part of stolon with bud and roots of *Platanthera dilatata*, magnified. *b* = apex of the bud; r^1 and r^2 = young roots; *r* = the tuberous root; *st.* = base of stolon. The dotted lines indicate the places where the sections have been laid.

FIGURE 3.—Transverse section of one of the two small mestome-cylinders of the stolon; letters as above. × 320.

FIGURE 4.—Transverse section of a mestome-cylinder from the tuberous root; letters as above. × 320. (Figs. 3 and 4 are both of *Platanthera dilatata;* fig. 3 of a specimen from Vermont, fig. 4 of a specimen from Mt. Elbert in Colorado.)