THE

AMERICAN JOURNAL OF SCIENCE

[FOURTH SERIES.]

ART. XLIII.—*Studies in the Cyperaceæ;* by THEO. HOLM. IV. *Dulichium spathaceum* Pers., a morphological and anatomical study.

THE monotypic genus *Dulichium* has quite a large distribution in the eastern part of North America, extending from Nova Scotia as far south as to the tropical Florida. It is a strictly hydrophilous plant, growing socially along rivers or on borders of ponds, in wet moss or in the water itself. But in spite of the very common occurrence of our plant there are, nevertheless, some points of morphological and anatomical interest, which have, so far, escaped the attention of the botanists. Although our plant possesses only a few characters, by which it is readily distinguished from its nearest allies, a general sketch may be of some importance in order to give a more complete idea of its entire organization. It is, altogether, the writer's intention to present in these cyperographical studies a number of details, observed in the various representatives, so as to collect some data, which might facilitate the study of the mutual affinities of the genera and species of this large group of plants.

In regard to the systematic position of *Dulichium* it is generally placed near *Cyperus* and *Kyllinga* on account of the two-ranked bracts of the inflorescence; but it differs from these genera by the presence of bristles in the flower and by the distinctly beaked achenia. It is, also, generally stated that *Dulichium* has only lateral inflorescences in contrast to *Cyperus* and *Kyllinga*, but this statement is, of course, not correct, as shall be demonstrated in the present article.

If we examine the underground part of *Dulichium* we observe a rather long, horizontal rhizome with sympodial ramification and reminding one very much of *Eleocharis palus-*

tris and others. The internodes are distinct and partly covered with rudimentary, sheathing leaves. Relatively strong roots develop above the nodes, especially from the lower surface. Several stems, above-ground, arise from the rhizome and they show a structure very different from what we are accustomed to see in the *Cyperaceæ*, having numerous cylindric and hollow internodes. As we remember the stem, above-ground, of the *Cyperaceæ*, it is generally solid and forms a distinct, often very long scape. Vegetative branches do not commonly develop upon the stem, above-ground, but we have noticed, however, a few cases where a small, horizontally creeping branch had developed from the axil of one of the stem-leaves. Such secondary branches showed the same kind of ramification and structure as the rhizome.

The leaves of *Dulichium* are either reduced to tubular sheaths upon the rhizome and at the base of the stems, or they are normally developed with a linear blade, a short, crescent-shaped ligule and a long tubular sheath.

By considering the inflorescence we find the flowers arranged biseriately in spikes. Each flower is perfect, supported by a scale-like bract, and has commonly eight downwardly barbed bristles, which are a little longer than the style of the ovary. The three stamens have long filaments and reach above the apex of the bristles. The style is papilliferous in its entire length like the two filiform stigmata; the achenium is at maturity oblong, flattened, shortly stipitate, and the remaining style forms a slender beak. By returning to the inflorescence, we have stated above, that the flowers are arranged in from six- to eight-flowered spikes, which again are arranged biseriately along a short rhachis, which is the continuation of a short peduncle, almost entirely inclosed by the sheath of the supporting leaf. The inflorescence consists then of one terminal and about eight lateral spikes, these last being supported by scale-like bracts, but destitute of any prophylla. A prophyllon, clado-prophyllon, is, however, to be observed at the very base of the peduncle; it is very short and tubular with the apex oblique. While this general structure applies to all the lateral inflorescences of *Dulichium*, it also agrees with the terminal one, with but one exception, that no prophyllon is developed at the base of the peduncle, this being the immediate continuation of the main stem itself. By comparing now the inflorescences of our genus with those of *Cyperus*, the difference consists merely in that they are scattered along the stem in *Dulichium*, while in *Cyperus* they are gathered towards the apex of the long scape. In this way the inflorescences in *Cyperus* form like an umbel with the outer (the lowest-situated) borne on longer peduncles than the inner ones, while the terminal inflorescence is almost sessile in the center of the umbel.

The terminal inflorescence in *Dulichium* is, on the contrary, the highest situated and is readily distinguished from the lateral ones by having no prophyllon.

The most important morphological peculiarity in *Dulichium* lies, therefore, in the structure of the stem with its numerous internodes of equal length, a structure which naturally influences the composition of the inflorescence, but in reality only differing from the related genera by the non-development of one of the internodes into a scape.

We will, thereupon, examine the internal structure of our plant, beginning with the foliar organs. The cauline leaves with well-developed blade show a structure which is very much the same, as we know from the literature, to be characteristic of the genus *Carex*. The epidermis of the blade shows a very uniform structure on both faces, the upper and the lower, and it seems to be a marked characteristic of *Dulichium* that hairs are entirely wanting and that epidermal thorns very seldom occur. It is only along the margins and along the keel of the leaf that such thorn-shaped expansions are to be found. The cuticula is rather thin and stomata are only present on the lower surface of the leaf-blade; they are slightly prominent, surrounded by four cells and form generally two longitudinal rows between the mestome-bundles. Concerning the shape and the size of the individual cells, the epidermis does not show anything of interest, except that some of the cells, which lie above the median mestome-bundle, are developed as "bulliform-cells." The peculiar internal cone-shaped projections, which we have recorded in our article upon *Carex Fraseri*, abound in the epidermis of the leaves of *Dulichium*. In regard to the cell-content of the epidermis, we were rather surprised to observe that tannin was present in several of the cells, and we succeeded later on in tracing this matter to various tissues of the leaf, the stem, the rhizome and the root. Antoine Mazel* deserves the credit for being the first author who detected the tannin-reservoirs in the genus *Carex*, a fact that is the more interesting since the *Cyperaceæ* formerly, like the *Gramineæ* and the *Ranunculaceæ*, were considered exceptional in not possessing reservoirs of any kind.

The mesophyll of the leaf consists of about four strata of closely packed palissade-cells on the upper face, while the remaining part of the mesophyll is built up by more or less irregular cells, which surround large lacunes, one between each of the two mestome-bundles. By studying the development of these lacunes in very young leaves, it was observed that they originated from the coalescing of a group of from four

* Mazel Antoine: Etudes d'anatomie comparée sur les organes de végétation dans le genre *Carex*. Genève, 1891. (Reviewed by the writer in the Bot. Gazette, February, 1892.)

to five colorless cells. Very characteristic of the mesophyll are the numerous and large tannin-reservoirs of long, cylindric cells, single or several connected together. These reservoirs are especially abundant just inside the epidermis of the upper face of the leaf, where we have counted no less than fifty reservoirs inside a stratum of about one hundred epidermis-cells. They are, also, quite abundant in the inner part of the mesophyll, around the lacunes, or bordering on the parenchyma sheath of the mestome-bundles. Concerning the general distribution of the mesophyll in the leaf, it appears, on examination of transverse sections, to form isolated groups between the larger mestome-bundles, which are supported, on both faces, by groups of stereome.

The mestome-bundles are all situated in a single plane in the leaf, averaging about twenty-five on each side of the midrib; they represent two forms, according to their size. The largest are the most numerous and differ from the smaller ones by a fuller development of their leptome and hadrome; otherwise the structure is identical for both. There is a parenchyma-sheath of thin-walled and usually colorless cells, inside of which is a constantly closed mestome-sheath,* the cells of which are slightly thickened. This inner sheath, by Schwendener called the mestome-sheath, was first pointed out by this author as characteristic of the *Cyperaceæ*, *Juncaceæ* and a number of *Gramineæ*.

The leptome and the hadrome are not separated from each other by thick-walled mestome-parenchyma, and both are well differentiated in the largest bundles. The hadrome contains generally two pitted ducts and a few ring-vessels. A small lacune is often to be observed above the ring-vessels.

Stereome is not abundant in the leaf, and forms only small groups above and below the larger mestome-bundles, while the smaller bundles are merely supported by this tissue on their hadrome-side; it does not occur as isolated groups excepting in the margins of the blade. The stereome was, in some instances, observed to surround tannin-reservoirs, especially on the superior face of the leaf.

Having now examined the structure of the assimilating leaf, we might in this connection consider the bracts of the inflorescence. There are, as stated above, really two kinds of bracts in the inflorescence of *Dulichium*, viz., those which support the spikes, and those which support the single flowers, but although their shape is somewhat different their internal structure is exactly the same. These bracts show a very firm structure due to the extremely thick-walled epidermis of the dorsal face, which is the only tissue that constitutes the broad, hyaline

* Schwendener S. Die Mestomscheiden der Gramineenblätter, Sitzungsber. k. Akad, Berlin, 1890.

margins of the bracts. No stomata are to be observed and the epidermis does not show any development of the so-called bulliform-cells. Epidermal expansions as thorns were only observed along the margin, and some of the epidermis-cells of the ventral face were found to contain tannin. There are usually only five mestome-bundles, which are very weakly developed, containing merely leptome and no vessels; the mestome-sheath is well-marked and is composed of thick-walled cells. There is only a small quantity of mesophyll in the bracts, and this forms isolated groups between the mestome-bundles, being composed of a few, two or three, layers of closely packed polyedric cells. Only a few tannin-reservoirs were observed in the mesophyll.

A much stronger development is shown to be possessed by the stereome. This tissue shows, however, the same distribution as we have seen in the green leaf, but it attains a more considerable size in the bracts, where it, also, occurs in several isolated groups, viz., on both sides of the midrib and near the margins.

The stem, above-ground, is, as we have shown in the preceding cylindric, hollow and distinctly jointed. It is perfectly smooth, since the epidermis is destitute of any projections. The epidermis shows, altogether, a very uniform structure like we have seen in the leaf, and we find, also, here the internal silicious cones in those cells which cover the stereome. Stomata are present, but rather scarce, forming merely a single row between the ribs on the free part of the internodes.

The green bark, the assimilating part of the stem, does not form any closed ring in *Dulichium*. It consists of closely packed polyedric or roundish cells, and forms, in transverse sections, isolated groups between the outer band of mestome-bundles. It contains only a small number of tannin-reservoirs, which are generally situated close to the large, round lacunes. These lacunes correspond in number and arrangement to the mesophyll, which borders immediately on their exterior side. Inside the ring of lacunes is a rather heavy layer of colorless parenchyma, the cells of which are large and roundish, and in which an inner band of mestome-bundles is imbedded. The center of the internode is occupied by a wide cavity, originated from the breaking down of the central mass of fundamental tissue. The nodes themselves are solid and largely built up of very thick-walled, star-shaped cells, which are conspicuously porose.

The mestome-bundles of the stem form, as stated above, two concentric bands, those of the inner being the largest. They are all collateral, and are surrounded by thin-walled parenchyma-sheaths; the leptome and the hadrome is well differentiated and sometimes separated by a layer of thick-walled mestome-parenchyma.

Stereome is well represented in the stem, where it occurs on the leptome-side of the outer mestome-bundles and on the hadrome-side of the inner ones. In this way it does not form any closed ring neither around the single mestome-bundle nor around any of the two bands of bundles, which, otherwise, seems to be quite common in the stem of the *Cyperaceæ*.

The peduncle, the spike-bearing stem, shows very near the same structure as we have observed in the main stem. There are, however, a few differences to be found, which may be noticed here in connection with the stem-structure, since such structural divergencies between stem and peduncle have not, hitherto, been studied very much. Grevillius,* Laborie† and Trautwein‡ are some of the few authors who have treated this subject, and their studies have shown us many interesting details in regard to the anatomy of the inflorescential axes in a number of plants.

In *Dulichium* the peduncle is strongly flattened in contrast to the cylindric stem, a fact which is due to its tight enclosure in the long leaf-sheath. It shows a relative firm structure in regard to the development of the mechanical tissue, and is solid, not hollow. The epidermis agrees very well with that of the stem, but is armed, however, with a few rows of thorn-shaped expansions along the two lateral margins. The stomata and the interior projections show the same structure and distribution as described above as characteristic of the stem. The bark-parenchyma contains chlorophyll and surrounds large lacunes, which alternate with a corresponding number of mestome-bundles.

These, the bundles, are arranged in a peripheral band; they are surrounded by a thick-walled parenchyma-sheath, and the leptome is often separated from the hadrome by mestome-parenchyma of thick-walled cells. The leptome occupies only a small part of the bundles, while the hadrome is more fully developed with several ring-vessels and generally two large pitted-ducts. The stereome forms large groups around the mestome-bundles. Tannin-reservoirs are, also, present in the peduncle, where they were observed in the bark close to the lacunes, but not in the large, colorless parenchyma, which occupies the center of the peduncle.

This is the general structure of the peduncle underneath the spike-bearing part, the rhachis, and we notice by examining this a certain change in structure, which is, especially, due

* Grevillius, A. I. Anatomiska studier œfver de florala axlarna hos diklina, Fanerogamer, Bihang Kgl. Svenska Vet. Akad. Hdlgr., vol. xvi. Stockholm 1890.

† Laborie, E. Anatomie des axes floraux Revue scientifique, vol. xliv, Paris, 1888.

‡ Trautwein, J. Ueber Anatomie einjähriger Zweige und Blüthenstandsachsen, Inaug. diss, Halle, 1885.

to the biseriate insertion of the flower-bearing spikes. A transverse section of the rhachis shows a change in regard to the outline, from almost flattened to semicylindric, while the minute structure at the same time shows some points of difference. The mestome-bundles have moved farther in towards the central, colorless fundamental tissue, and most of them have lost their outer support of stereomatic tissue. It is only on the concave side of the rhachis that the stereome is well developed so as to form supporting layers for the mestome-bundles. The mesophyll shows the same structure as in the peduncle, and it contains several lacunes of rather irregular size and shape.

Very different from the peduncle and the rhachis in regard to shape and structure is the rhacheola, the axis of the flower-bearing spike. It is broadly winged from the decurrent margins of the bracts and shows a very simple anatomical structure. The epidermis contains tannin in great abundance, and the inner tissue is largely composed of a colorless parenchyma in which two or three small mestome-bundles are imbedded. These are partly surrounded by a single layer of stereome besides by a thick-walled parenchyma-sheath; the elements of the leptome and the hadrome are well differentiated.

Having examined the aerial stem of *Dulichium* with the peduncle, the rhachis and the rhacheola, we will now proceed to the stem under-ground, the rhizome. The entire structure of the rhizome does not show any considerable strength in development, which is evidently due to the fact that the soil in which our plant grows is generally very soft and loose, and does not make any great resistance necessary. The epidermis shows naturally a much more simple structure than we observed in the stem above-ground, being deprived of stomata and epidermal projections. The cell-content is on the other hand not only represented by tannin, but also by large deposits of starch. Inside the epidermis is a broad layer of thin-walled bark-parenchyma, filled with starch, besides that tannin-reservoirs are to be seen in the outermost layers, close to the epidermis. The bark contains only one, but very large lacune, which occupies the greater part of the dorsal, the upper part of the creeping rhizome. The innermost stratum of the bark-parenchyma is differentiated into a completely closed endodermis, which, from the manner in which the cell-walls are thickened, represents a typical U-endodermis. A large, starch-bearing fundamental tissue is to be observed inside the endodermis, and it is here that the mestome-bundles are situated.

These, the mestome-bundles, are all well-devoloped, but are not arranged in any order; they represent two forms, viz, collateral and concentric or, in this case, perihadromatic, since

the leptome is partly surrounded by the hadrome. This form of bundle, the perihadromatic, is not uncommon in monocotyledonous plants, while the perileptomatic type is especially characteristic of the Ferns.

The mestome-bundles, the collateral and the concentric, show a still more advanced development in the rhizome than in the stem above-ground, viz., the hadrome has a greater number of pitted-ducts and the leptome-groups are much larger.

The innermost part of the central-cylinder is, as stated above, occupied by a mass of starch-bearing fundamental tissue. The stereome is rather poorly developed in the rhizome and its cells are rather thin-walled. It is here restricted to the mestome-bundles which it partly surrounds, and it seems to be strongest developed on the hadrome side, the inner face of the bundles. Numerous tannin-reservoirs were observed to be scattered around in the groups of this tissue, the stereome.

We have now pointed out the principal anatomical characteristics of the leaf and the stem with their various modifications, such as they are represented in our genus, and we might finally give a brief sketch of the root, although this was not observed to possess any peculiarities so as to be distinguished from that of the majority of the other *Cyperaceæ*. There is, inside the epidermis, a single layer of very thick-walled cells, which form a closed ring around the broad bark-parenchyma, in which a few tannin-reservoirs are to be seen. The bark shows the characteristic tangential collapsing of some of the cells, and its innermost layer is differentiated as an endodermis. The pericambium consists merely of one layer of cells, which are interrupted here and there by the protohadrome. The center of the root is occupied by two very large vessels, which alternate with the corresponding groups of leptome.

Washington, D. C., December, 1896.

EXPLANATION OF FIGURES.

Anatomy of *Dulichium*.

FIGURE 1.—Transverse section of the median part of the leaf-blade, showing the bulliform-cells above the median mestome-bundle. × 320.

FIGURE 2.—Transverse section of epidermis of leaf, showing a silicious cone inside one of the epidermis-cells. × 400.

FIGURE 3.—Tannin-reservoirs in the mesophyll and in the stereome from a transverse section of the leaf-blade, the upper face. The black-painted cells indicate the tannin-reservoirs in this as well as in the other figures. × 240.

FIGURE 4.—Tannin-reservoir in a group of stereome from the superior face of the leaf-blade. × 400.

FIGURE 5.—A large mestome-bundle from the leaf-blade, transverse section. Three of the epidermis-cells contain cones, and tannin-reservoirs are observable in the mesophyll. × 320.

FIGURE 6.—Transverse section of a small mestome-bundle from the leaf-blade. × 320.

FIGURE 7.—Transverse section of a bract, showing a mestome-bundle, a large group of stereome and a tannin-reservoir. × 320.

FIGURE 8.—Same section, showing the midrib and a part of the margin, which only consists of the dorsal epidermis. × 60.