DEGREE CONFERRED

1909

ON THE ANATOMY AND PHYSIOLOGY OF THE ENDODERMIS.

A Thesis Written For The Purpose Of Obtaining
The Degree Of Master Of Arts, At The University Of Manitoba.
A. D. 1909.

by

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Historical Review.

As far back as 1858 Caspary (1) observed in Elodea Canadensis what he describes as:

"A single row of cells, closely joined together, which by this arrangement alone differentiate from the other cells of the cortex and vascular tissue, which are not arranged regularly in closed rings."

"Besides this, however, the cells of this row show in cross section on the centre of their side walls a dark point. These points consist of very small, oblong, pit-like markings of very indistinct outline."

Caspary gave this ring the name "Schutzscheide" or "Vagina tutelaris," because, he adds, "It serves to protect the vascular system of the plant."

In 1865, however, he corrected himself, and wrote:

"The drawings are right, but I am convinced that the explanation is not correct."

"The dark points, as shown by tangential sections, are formed by a wavy shape of the side-wall, which shape stands out especially if the sections are treated with sulphuric acid or caustic potash."

Sanio (3) connected this layer with the phenomenon of secondary growth, and called it "Verdickungsring," because he sought in this layer the origin of the cambium for that growth. He rejected the name Schutzscheide, because it is broken by the increase in thickness in cases as the Berberis.

In 1865 (4) he followed up his criticism by showing that cells, marked by these dark points, are also found in the corkcells of Melaleuca imbricata, Callistemum lanuginosum and others, so that the presence of this mark would not be sufficient to identify a layer of cells.

In 1867 and '68 Pfitzer (5) published a thorough study of this layer of cells in the Equisetaceae.

His paper shows very interesting drawings of the cells of this layer, proving that all along the radial and horizontal cell walls there is a continuous brown band of a substance which resists the action of Sulphuric Acid. In this way it is even possible to get pieces of the skeleton of this layer by eating away the surrounding tissue with stong sulphuric. Very interesting points are brought forward by this paper, to which I shall refer later on, in connection with my own investigations and original drawings.

Russow (6) studied this region in several plants and explained the spots of Caspary by the formation of a cork-band on the cell wall.

He called the tissue in this particular region generally "Kritenchym" or "Scheidegewebe," which may appear as:

1 Schutzscheide, consisting of thin walled cells with the "points of Caspary."

2 Steifungsscheide; when all cell walls are thickened evenly.

3 Stützscheide; when the thickening is irregular, and often appears in several rows of cells.

In 1877 Caspary (7) defined again what he means by his "Schutzscheide," especially against a criticism offered by Falkenberg (8), that to many different tissues this name is given.

Caspary's definition reads as follows:

"Es ist diejengie Schicht, die, eine Zellage dick, auf den seitlichen, oberen und unteren Wanden zum Theil gewellt, stets verkorkt (oder verholzt,) ohne Zellzwischenräume, entweder das System der Leitbundel im Ganzen, oder die einzelnen, gleichviel ob in Stamm, Wurzel oder Blatt, umgibt."

Against Sachs' (9) criticism, that the word Schutzscheide says more than can be justified, and that Strangscheide is a better name, Caspary brings up, that Sachs himself (9, page 35) says that in case some tissue serves as "Schutz" for others, part of the cell walls is changed into cork or cuticle, while he answers Sachs' objection that the word Schutzscheide is over loaded with "Zischlauten" with the remark that that word contains the same amount of "Zischlauten" as the name "Julius Sachs."

Klinge (10) in 1878, published a comparative study of Gramineae and Cyperaceae in which he calls the points of Caspary "Verdickungsfalte" and shows that their formation in different plants takes place in different times of life. In some cases (Lolium temulentum) it is not visible even when the protophloem and protoxylem have been completely differentiated.

In Erianthus Ravennae and Eulalia japonica he found in the cell wall of the thickened endodermis, which in that case he calls "Stützscheide," protuberances of silica. (The method he used is as follows: make sections not too thin; boil in Schultze's mixture (17, p. 213); boil and wash in distilled water; next in alcohol; glow for 30 - 40 min. on slide above platina and examine in a drop of hydrochloric acid.)

Schwendener (11) gave in 1882 an extensive study of the Schutzscheiden."

1. Anatomical features are: the mechanical power of resistance; the continuity of the form of the cross section and the relative impermeability of this layer.

The points are, according to him, chiefly due to a waving of the side walls owing to a decrease in turgor, when the section is made.

2. Conditions of permeability. In many plants the inner and outer tangential walls are clear cellulose, and so are the radial walls with the exception of a single band of cork.

Although microchemical reactions do not shed any light upon the physical properties of the membranes, still when the sheath is full grown, it is less permeable than the ordinary tissue.

Schwendener made experiments with a solution of Iodine, which coloured the stareh of the cortex in rhizomata of Triticum repens, Convallaria majalis and others right away, but penetrated only after several hours into the sheath and the inside tissue.

A solution of tannin in the vessels of Iris germanica produced the iron reaction in the inside tissue, but not in the cortex.

3. In some cases, where the cells of the sheath were very much thickened, Schwendener found permeable transmission cells, which have tender walls, with the exception of the cork band. In longitudinal sections they sometimes appear like a row of stomata (Iris germanica) or may be arranged in a continuous row (Renanthera coccinea) which in some cases is from 6 - 10 m. m. long (Cypripedium venustum.)

In roots of Iris germanica and Iris florentina, and of Convallaria majalis he found, after taking away the outside cortex, that chlor-zinc-iodine penetrated to the vessels after about 1½ hrs., while the cells of the sheath itself did not show any coleuration.

Schwendener draws the conclusion that the re-agent must have entered by these transmission cells:

"Es sind das gleichsam die offenen Seitenschleusen eines Berieselungssystems, als dessen Hauptadern die groszen gefässe fungiren."

4. Mechanical strengthening of the sheath. The author then discusses the different ways in which the sheath may be strengthened:

a. by thickening of the cell walls of the sheath cells or of neighbouring layers (Ferns.);

b. by a combination of these two cases (Carex curvula);

c. by a separate ring of thick walled cells, parted from the sheath by a layer of ordinary cortex cells, 2 or 4 cells in thickness (Aroideae, Raphidophora).

5. The formation of cork on the membranes of the endodermis cells from a mechanical point of view.

The general opinion being, that membranes, provided with cork had an increased elasticity, Schwendener comes to the conclusion, that either the qualities change by the use of reagents, or there is no increased elasticity. On the contrary, there is more stiffness in the side wall.

That is also the reason of the waving of the elastic wall as soon as the turgor of the cell ceases, a phenomenon increased by the use of caustic or strong sulphuric.

6. Relation to Climate and Environment.

In plants, growing on rocks, walls, etc., which have to provide against long periods of drought, the sheaths are strong (Asplenium ruta muraria, Scolopendrium officinarium, Carex rupestris, e. a.)
In plants growing in places that are continually moist the sheath has weak, thin cell walls (Asplenium filia femina, Osmunda regalis, Marsilia, Typha, etc.)
Others, which take a position between the extremes, have the cell walls of the sheaths more or less strengthened (Carex, Juncus, etc.)

7. Development.

Schwendener gives different ways in which the sheath may develop, either from a true cambium (Juncaceae, Cyperacaea), a procambial tissue (Convallaria), a cortical parenchyma of which the inner cell forms the sheath or, as in the roots of Equisetum, the innermost but one.
His conclusion is, that a natural division of the tissues depends only upon their construction and function, and not upon the variable ontogenetical relations.
Van Wisselingh (12) made a very careful study of the structure of the tangential and cross walls and found that the corkband exists in the younger stages in all Phanerogams. He found, that the point of Caspary is not only due to waving of the walls, but that there is also a different refraction of the light.
In radial sections the band on the cross walls is only visible as a narrow yellow line, because these walls are not undulated, but the fact that it is still visible, shows that it is not only due to undulation as argued by some authors.

In the cell walls there is one part that is not changed into cork, the so-called middle lamella, the remnant of the primary cell wall. This membrane can be made visible by Höhnel's reaction (18, p.632) which consists of heating the sections with potassiumchlorate and nitric acid. This loosens the secondary corkmembrane and leaves the lamella visible. On further heating yellow balls of suberic acid may be observed.

Van Wisselingh explains the undulation of the secondary wall by the increase in volume, due to cuticularisation, and change into cork, which same question is brought up by Ed. Strasburger (19, p. 146 199, 210)

Development.

In young stages the spot of Caspary is a yellowish line along the tangential and cross walls, and also a little spot on the inside and outside corners to which the cell-contents attach themselves, and which are resistent to sulphuric acid.

Gradually the cork-membrane spreads over the whole cell wall. The spot of Caspary is at this stage not visible without reagents but is colored brown upon application of Iodine and strong sulphuric acid.

The middle lamella is not suberified, but shows itself as a very tiny colorless line, visible only with high power.

In still older stages secondary layers are formed, which show the lignine reaction with phloroglycine-hydrochloric acid (17, page157

Hugo de Vries (13) published in 1886 a study on the course of water in roots.

1. The Endodermis as Pressure line in Roots.

a. Physiological.

The material used were principally roots of Iris pseudacorus. De Vries connected long pieces of roots, the ends of which were cut off about 1 c. m. from the vegetation point, with a mercurial manometer and found that airbubbles passed out at 3 c. m. mercurial pressure.

This proved that the pressure in the parenchyma of young roots does not differ much from 1 atmosphere.

By strong pressure on the root, this pressure is transmitted from the older parts to the youngest ends without considerable loss. This conclusion is independent from the question in which part of the root this pressure is produced.

The top of a root of Iris, 12 c. m. long, was subjected to a pressure of 35 c. m. of mercury. The epidermis and exodermis at 2-2.5 c. m. from the vegetation point were cut away, but no water came through the side.

Every quarter of an hour another tangential section was taken off and examined under the microscope, but only at the 6th section a drop of water appeared through the endodermis.

As soon as the whole top was cut, water appeared from all the vessels Roots of Dicotyledons (Dipsacus sylvestris) and stalks gave the same results, n. l. that even by large difference in pressure the water is not forced fro the vessels into the intercellular spaces of the parenchyma.

Anatomical.

The mesh work of Caspary is always found in the endodermis, and is the real characteristic of that sheath. The cells of this layer have a very large turgor. (In sections that are not too thin, some cells may not have been touched, while the neighboring cells are all cut. The cells that are intact assume in that case a spherical form, owing to the counterpressure being taken away.) The protoplasts cleave strongly to the bands of cork, and so prevent the passage of water.

Against Schwendener's statement that the endodermis did not prevent the passage of his reagents, De Vries submits that the former always used poisons, such as tannic acid, iodine, etc., which killed the protoplasts. By using eosine, De Vries got the opposite results.

2. The Course of Water in Roots.

If the water from the roothairs and parenchyma of the cortex passes into the stele by action of the living protoplast only, there must be the additional evidence of protoplasma-currents.

De Vries actually observed these currents in radial sections of Tea Mais, Typha e.a. at from 2-6 c.m. from the vegetation point.

Higher up, where the corklayer is formed this current lessens, but was still visible a distance of 30 c.m. upwards.

Van Tieghem (16) gives a full theory of the division of the primary tissues in Epidermis, Cortex and Stele, and calls the inner layer of the cortex, the Endodermis, which is formed in roots as the Schutzscheide, in stalks as the Schultzscheide or as Starkescheide with their different variations.

Against criticisms from different sources he says, however, in 1891 (14) "Il faut se garder de faire entrer l' existence du cadre suberise on lignifie et des plissements qu'il porte, dans la defenition meme de l'endoderme."

L' endoderme n'est pas un tissue particulier, plisse on antre; c'est une region anatomique."

Schoute (15) contends that if the division of the primary tissues by Van Tieghem shall have its full value, the division into the three times must be proved by the embryology.

He investigates very carefully and fully whether the division into Dermatogen, Periblem and Glerom by Hanstein agrees with this division in the full grown tissues.

(I have not been able to see the original papers of Hanstein, mentioned under numbers 20 and 21, but might refer to Schoute (15) and Strasburger (17) as to Hanstein's division.)

Schoute comes to the conclusion (15, page 163) that in a few cases in which Hanstein's division is very clear, the meristematic layers do not always agree with the primary tissues of Van Tieghem, and further that Hanstein's division cannot claim morphological significance.

In the second part of his study "The Stelar-theory and Comparative Anatomy," Schoute gives a full list of Gymnosperms, Monocotyledons and Dicotyledons in which an endodermic has been either found by himself or recorded in the literature on the subject.

His conclusions are:

"That the division between Cortex and Tentral cylinder in stalk and root is distinctly marked by the general presence of a specially constructed Endodermis," and further

"That in stalk and root of vascular plants there is only one type of Stele, n. l. "Monostelie."

Observations of the Endodermis in Equisetaceae.

The Equisetaceae form a very clear and instructive material for the study of the endodermis.

In some species (E. limosum, E. debile) there is an endodermis round each stele, in others (stalk of E. hiomale) we find a double endodermis surrounding the ring of fibto-vascular bundles. Equisetum hiemale is of particular interest in the study of the meaning of the endodermis, because in this species we find in the stem a double collective sheath, but in the rhizoma a separate sheath round each stele.

The point of interest in this case is the spot in which rhizoma and stem meet, because if the endodermis is of physicological value, and, as we surmise from the literature quoted so far, may be the region which keeps the water from leaking mechanically from stele to cortex, there must be some arrangement for the transition from a collective sheath to the separate sheaths.