DEVELOPMENT OF THE TMESOPSIDA AND PTEROPSIDA LEAVES AND HISTOGENESIS OF THE EPIDERMIS

I. MARÓTI

Botanical Institute of the Attila József University, Szeged
(Received July 30. 1966)

Introduction

The morphogenesis of leaves, the development and structure of epidermis and stomata reflect in many cases the degree of development and natural taxonomic place of the species and family. The problem of the histogenesis of epidermis has been in the centre of interest for about a hundred years. The first examinations concerned mainly the genesis of stomata. The first observations concerning the development of stomata are connected with names of OUDEMANS (1866), HILDEBRAND (1866), PRANTL (1872) and STRASBURGER (1867). OUDEMANS (1866) could not, as yet, form a decisive resolution in connection with the peculiar development of stomata of the *Anemia species,* therefore he thought on four possibilities of the development. HILDEBRAND (1866) has already examined the development of stomata of more ferns, being anxious to discern some types. He named his types after the species. These types cannot be generalized, they are mechanical in nature, without reflecting the development. STRASBURGER (1867) and PRANTL (1872) have tried to give the first rule of the genesis of stomata with a universal validity. On the basis of their investigations two main types may be distinguished:

The guard mother cell develops with a single division from the primary mother cell.

The cell, left over in the middle part of the cell after a series of divisions of different directions in the primary mother cell, becomes the guard mother cell.

It became, however, evident in the course of later examinations that a number of plant groups cannot be included in the main type considered to be of general validity. PRANTL (1872) and STRASBURGER (1867) included the *Pteridophytae* and *Gymnospermata* incorrectly uniformly in the first group as but a number of classes may have been included here. This formulation allows of several misunderstandings.

The conclusions concerning the development of the epidermis of the several species are durable and highly useful in the synthetizing work. From the many literary data author mention but those treating of the *Pteropsidae.* RAUTER

(1870) compared the stoma development of *Niphobulus linqua, Anemia fraxinifolia* and *Pteris longifolia.* PRANTL (1881) observed, in the course of his anatomic and taxonomic examination of *Schizaeaceae,* even the formation of stomata of the *Schizaea pennula.* Britton and TAYLOR (1909) treated also of the formation of leaves and development of stomata of the *Schizaea pusilla.*

In the examination of histogenesis and historical development of stomata considerable results have been achieved by FLORIN (1931, 1933), who has distinguished, in the course of his examinations of the epidermis of *Coniferales* and *Cordaitales,* three main types of the history of development of the genesis of stomata:

A) The primary mother cell (of guard cells) becomes immediately guard mother cell.

B) The guard mother cell is, after the formation of the dividing wall, adjacent to the primary mother cell.

C) By the prepared division of the primary mother cell the guard mother cell precedes the development of the adjacent cells.

FLORIN (1933) mentions only two types in his work dealing with *Cycadales* and *Bennettitales:*

A) Haplocheil type:

1. The primary mother cell of guard cells functions immediately as a mother cell of these cells. This guard mother cell is divited by a longitudinal wall into two guard cells.

2. The adjacent lateral epidermal cells, which are equivalent to the primary mother cell, become mother cells of the adjacent cells. These are divided into accessory and coronal cells, or they are functioning immediately as subsidiary cells. The lateral adjacent cells are, therefore, perigenous.

3. Also the adjacent polar cells are perigenous.

B) Syndetocheil type:

1. The primary mother cell of guard cells is, as a rule, divided into three cells the middle one of which becomes the guard mother cell. Both lateral adjacent cells are of mesogenic origin and divided, sometimes, into accessory and coronal cells. The quantity of lateral adjacent cells may be greater on one side of the guard cells than on the other one.

2. The lateral adjacent cells (subsidiary and coronal cells) of perigenous origin are missing.

3. The adjacent polar cells of mesogenous origin are missing. Polar cells of perigenous origin may often come into being.

FLORIN (1931, 1933) deserves merit for demonstrating the first time the types of history of the development of stomata. He has tried to elaborate a unitary nomenclature for stomata. It is, anyhow, a failure in FLORIN's establishments that his definition of the types of development of stomata is not unambiguous:

A) He uses the notion of primary mother cell without explaining what he means to say. By the primary mother cell he means a dermatogenous cell similar (in size, shape, plane of cell division) to the adjacent cells, of which a stoma develops. Then, in the first division, the types (A) and (B) must be contracted

as the guard mother cell is adjacent in both cases inside the primary mother cell. Is, however, the primary mother cell differring from the other dermatogenous cells, so it is difficult to distinguish between the primary mother cell and guard mother cell, and we may not speak about haplocheil and syndetocheil types.

B) FLORIN's (1931, 1933) main historical types of the development of stomata may not be generalized for more taxonomical plant groups.

C) FLORIN has not treated of the site of stoma formation, the shape and plane of cell division.

In recent times a literature treating of the histogenesis of epidermis of *Tmesopsidae* and *Pteropsidae* is unknown. The first observations were not free from some original difficulties. A lot of observations are not exact enough, they have examined a species picked out at random, without comparing families. The figures published by BRITTON and TAYLOR (1909) HILDEBRAND (1866) and PRANTL (1881) are schematic. From the few data of examination there cannot be seen wether or not the form of the development of stomata is connected with the degree of development of the family and species. On the leaf-primordium we cannot find any references in the literature concerning the site of the genesis of stomata. Any exact observations concerning the cell division and chromosomes, as well as any phographic figures, are unknown in the literature.

Materials and Methods

During my examinations (1961) I have observed the development of leaves of the following young species being in division:

1. *Psilotum nudum* (L.) GRISEB.
2. *Tmesipteris elongata* DANG.
3. *Ophioglossum crotalophoroides* WALT.
4. *Botrychium multifidum* (GMEL.) RUPR.
5. *Marattia salicina* SM.
6. *Osmunda regalis* L.
7. *Schizaea dichotoma* (L.) SM.
8. *Anemia rotundifolia* SCHRAD.
9. *Stromatopteris moniliformis* METT.
10. *Asplenium viride* HUNDS.
11. *Loxsoma cunninghamii* R. BR.

We have got the material from the hothouse and herbarium of the *V. L. Komarov Botanical Institute in Leningrad,* from the botanical gardens of the *Botanical Institute of the University in Szeged,* as well as from my own collection in Poland. The preparations were made according to the previous papers (MARÓTI 1961).

Results

A) PSILOTACEAE

1. Psilotum nudum (L.) GRISEB.

VETTER (1951) and WARDLAW (1957) have dealt with the formation of shoot and leaf of *Psilotum.* During our examinations we have observed only the development of the epidermis and stoma of the shoot. On the apical meristems of shoot the dermatogenous initials and dermatogen consist of undifferentiated,

isodiametrical cells of big nuclei. The cells are in active division. This region takes place on the apex 350—420 μ wide. The length of the dermatogenous cells is 19—24 μ. Their width is 15—22μ. The mean area of a dermatogenous cell is 378 sq. μ.

Below that region takes place the organization zone in a strife of 280—330 μ width. The guard mother cells here are formed and divided into two guard cells. The dermatogenous cell is divided into two cells of nearly equal size: the guard mother cell (Gm) and the epidermal mother cell (Em). The plane of cell division is almost straight. The genesis of stoma is euhaplocheil, its structure is acyclical.

2. Tmesipteris elongata DANG.

(Fig. 1)

Morphogenesis of the leaf

The formation of leaves of the *Tmesipteris* is treated of by BOWER (1935). Later WARDLAW (1957) has carried out, in absence of a dividing shoot, the comparison of the formation of leaves of Psilotum and Tmesipteris, on the basis of BOWER's (1935) examinations and drawings.

In the course of our examinations we have observed a shoot in vigorous division. The apex is of elliptical shape, showing several multicellular knobs. The apical meristems are well developed and somewhat defended by the lateral leaf-primordia.

We have to correct BOWER's (1935) and WARDLAW's (1957) results according to wich „the summit of the primordium in *Tmesipteris,* as seen in a radial longitudinal section, is occupied by a single larger cell of a wedge-like or prismatic form (BOWER) and unlike *Psilotum,* this apex retains its meristematic properties and potentialities".

We have, namely, found so during our examinations that the superficial cells on the multicellular knob of apex lose their meristematic potentialities after a few divisions.

The multicellular summit may have one apex (developing a foliage leaf), and it may have also three apexes if between the two apexes another apex appears rounded off and centrally as compared to the plane of cell division (developing a sporophyllum-shoot). The multicellular summit loses its divisibility at the formation of the leaf-primordium and hasn't any more role in the formation of the leaf.

A 0,5—4 mm long sporophyllum primordium functions in the same way as a shoot of limited growth. On the „apical meristems" of the sporophyllum primordium (on the multicellular knob of the apical meristems of the shoot) there develop two tubers of identical size the end of which has lost the potentiality of division and transformed into „apiculus", a spinelike outgrowth. Between the two sporophyllum knobs there appears a little centrally a rounded off sporangial knob derived from the apical meristems of the shoot. The apical meristems of the sporophyllum primordium developed in that way produces the leafstalk of sporophyllum (shoot!) and the two leaves.

Formation of the epidermis

The differentiation of shoots and leaves is reflected well by the formation of epidermis, the change of the size of epidermis cells, the place of appearance of stomata. Examining the formation of epidermis of the primordium of the Tmesipteris leaf and sporophyllum shoot we can observe a zonal arrangement. This zonal arrangement coincides in many respects with the zonal arrangement established by WARDLAW (1957) for shoots.

I have carried out many measurements and observations for determing and characterizing the single zones of the epidermis formation. I have measured the length and width of cells, their surface, the proportion of nucleus and cell content, observing also the shape of cells, the thickness of the cell-wall, the number of cells that have been dividing, the site of formation of the guard mother cells and guard cells. These examinations were carried out from the distal apex to the basis. The change of the area of cells is represented graphically from the apex to the basis. On the absciss the length of leaf is given in μ, on the ordinate the size of the cell area in the unit of $\mu^2/10$.

Taking into consideration these cytologic studies, the following zonal regions may be distinguished, in basipetal order, on the primordia of leaves and sporophylla:

(1) Distal part (apiculus of the leaf). The length of this region is 500—1400 μ. On the apical meristems of the shoot, in the time of the genesis of the multicellular knob, the superficial cells are repeatedly divided with anticlinal walls, they lose, however, soon their meristematic activity, become longer, their walls become secondarily thicker, the cells become vacuole. The size of cells decreases gradually from the summit of apiculus till the basis. The apiculus ensures the defense of cells below itself and, on the other hand, it defends the apical meristems of shoot.

(2) Sub-distal part. It takes place in a strife of 300—400 μ width below the distal region. It contains the group of embryonal initial cells. This is the centre of the meristems. The dermatogen developed here consists of undifferentiated, isodiametrical cells of big nuclei. The cells are in an intensive division. That separetes cells in the beginning also distally, later on, however, only proximally.

(3) The organogenetical part takes place in a strife of 300—500 μ width, below the subdistal region. It may be observed in that part which cells become guard mother cells and they are divided here into two, forming guard cells. The dermatogenous cells already elongate here.

(4) The sub-apical region is characterized by the vertical elongation of the epidermis cells and the powerful increase of the guard cells. The cell valls begin secondarily to become thicker and the radial walls get wavy.

These regions may, however, not be separated by cytologically rigid, sharp limits, the single regions pass over to one another.

Formation of the stomata

The guard mother cells (G. M. C.) are produced in the subdistal region with halving division, they can, however, be recognized but in the organogenetic part. In the organogenetic zone the guard mother cells enlarge, getting a little rounded off form. Then the guard mother cells are divided in two, parallelly with the longitudinal axis of the leaf, being transformed into guard cells (G. C.) The axis of division is nearly straight. We call this stoma formation to be of euhaplocheil origin.

The adjacent mother cells surrounding the guard mother cell become immediately epidermis cells. There aren't formed any subsidiary cells, therefore the stomata are acyclical.

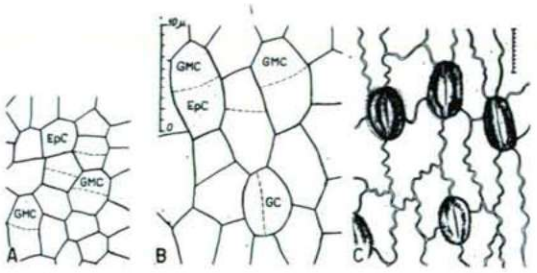

Fig. 1. Development of the *Tmesipteris elongata* DANG. stomata. G. M. C.=guard mother cell, Ep. C.=epidermal cell, G. C.=guard cell, A—B=dermatogen during division, C=consolidated epidermal detail.
Length of the consolidated guard mother cell (G. M. C.) 35—38 μ,
Width of the consolitated guard mother cell 33—38 μ,
Length of the G. M. C. during division in two: 46—57 μ,
Width of the G. M. C. during division in two: 35—45 μ.

B) OPHIOGLOSSACEAE

3. Ophioglossum crotalophoroides WALT.

The formation of the leaf shows a temporal division into sections instead of a spatial zonation. The leaf-primordium is divided in its full size. At the rim of the leaf-primordium, in a strife of 300—800 μ width, the division is more intensive than in the middle part of the leaf-primordium. At the rim of leaf-primordium the distal region is not separated, either.

The dermatogenous cell is divided with a nearly halving division into two cells: guard mother cell and epidermal mother cell. The axis of division is mildly concave or straight. The produced two cells may be of equal size or the guard mother cell is smaller than the epidermal mother cell. The guard mother cell is prevailingly produced from the distal end of the dermatogenous cell; anyhow, it may be produced also from its proximal and lateral parts. The genesis of stoma is a transition from the euhaplocheil type to the haplocheil one, its structure is acyclical. In the case of some *Ophioglossum* species accessory cells may be produced in a perigenous way.

Dimensions of the dermatogenous cells: 21x23 μ. Dimensions of the guard mother cells: 22x23 μ. Dimensions of the guard mother cell divided in two: 28x30 μ. Dimensions of the consolidated guard cell: 70x73 μ.

4. Botrychium multifidum (GMEL.) RUPR.

In the course of the formation of leaves the subdistal, organization and alongation zones cannot be separated sharply from one another. The leaf-primordium is divided, differentiated, and elongated nearly in its full size. If we examine the percentage of division from the rim of the leaf-primordium to its middle, zones may be observed which flow together.

At the rim of leaves a unilinear distal region is definitely separated. Size of the cells of the distal region: 26x35 μ. During the formation of leaf the vascular bundles are differentiated at first.

The formation of the stoma shows a temporal periodicity instead of a spatial zonation. Apart from the consolidated stomata also guard mother cells in the state of development can be found. The dermatogenous cell is divided with a nearly halving division in two cells: guard mother cell and epidermis mother cell. Between the two cells the axis of division may be straight or mildly concave. The produced two cells may be of equal size; the guard mother cell is, however, frequently smaller than the epidermis mother cell. Around the produced guard mother cells the dermatogenous cells are in an intensive division. The guard mother cell is dominatingly produced from the distal and of the dermatogenous cell; it can, however, be produced from its proximal and lateral parts, as well. The genesis of stoma is haplocheil (at some *Botrychium* species it is a transition between the euhaplocheil and haplocheil types), its structure is acyclical.

Size of the dermatogenous cell: 23x31 μ. Size of the guard mother cell: 17x23 μ. The size of the guard mother cell during division: 19x26 μ. Size of the consolidated guard cell: 38x51 μ.

C) MARATTIACEAE

5. Marattia salicina SMITH.

(Fig. 2)

The formation of the epidermis of leaves does not show any definite zonal separation. At the rim of a leaf primordium of 2—20 mm size, in the width of a cell line, the distal region may be observed. In this region 17 μ long and 13 μ wide cells may be found. The distal radial wall of the cells is thicker and the nucleus takes place in the proximal end of the cell. That layer is less divided and defends the meristematic cells below itself. Below the distal region, in 5—8 cell lines and 35 μ width, the dermatogenous initials, the subdistal region can be observed. The subdistal region cannot be sharply separated from the organization and elongation zones as even the leaf-primordium of 20 mm size is divided, differentiated, forms guard mother cells on its whole surface, and the cells elongate in the meantime, as well.

The leaf primordium produces, in the course of the division of its whole surface, dermatogenous cells in definite number, size and shape which are characteristic of the species, and in the same way guard mother cells and accessory mother cells. Then the cells elongate on the whole surface and get, with the definite size of the leaf, into the phase of ripening. In the development of the epidermis of *Marattia salicina* the temporal zonation dominates over the spatial one.

Formation of the stomata: it is preceded by production of cells of characteristic shape and formation that perform the early gas exchange. We called these cells which are unknown in literature „gas exchange hose" cells. These cells are, viewed from above, 3—5 angled (with outer tangential walls), and 4—7 small rounded off holes (perforations) of 0,5—1,5 μ diamser may be observed in their outer tangential walls. These cells enlarge towards the mesophylum, get an ovate or hose shape, their cell wall is thoroughly thin. Size of the gas-exchange hose cells viewed from above the outer tangential wall: 10x11 μ, the inner tangential wall: 26x32 μ, and their size of (radial) depth: 24—28 μ.

These cells serve as substitute for the gas exchange of the primordium that has reached a considerable size, without, however, containing developed stomata. In the gasexchange hose cells of the developed leaf quartz is stored, and so they become quartz cells.

The formation of stomata begins in the bilateral dermatogenous area of the leaf vessels, then it extends also over the intervasculary area of leaves. One of the dermatogenous cells of the organization region, in the phase of division, the primary mother cell, is divided in two cells, forming a little concave cross cell wall; the distally located cell becomes the guard mother cell, and the basally located one becomes the polar adjacent mother cell. The guard mother cell is often smaller than the polar adjacent mother cell. Around the guard mother cell the dermatogenous cells are in an intensive division. The adjacent mother cells begin to divide parallelly to the surface of the guard mother cell. The axis of division is mildly concave. The subsidiary cells are produced in a perigenous way. We call this form of the genesis of stomata to be of haplocheil type and of amphicyclical structure.

The guard mother cell is surrounded by 4—5 adjacent mother cells. From these two-three become lateral adjacent mother cells and two ones polar adjacent mother cells. Dimensions of the stoma mother cells after their formation: G. M. C. = 9x12 μ, A. M. C. = 13x17 μ.

Then the guard mother cells enlarge, the adjacent mother cells begin to divide parallelly at the periphery of G. M. C. into lateral subsidiary cell and lateral coronal cell, forming polar subsidiary cells and polar coronal cells as well.

Size of stomata in the time of the division in two of the guard mother cell: G. M. C. = 17x28 μ, L. S. C. = 5x20 μ, L. C. C. = 8x20 μ, P. S. C. = 8x26 μ, P. C. C. = 9x24 μ.

In the following the guard mother cells are divided in two by a longitudinal wall, become guard cells, then they enlarge and compress the adjacent subsidiary and coronal cells around themselves.

The adjacent protodermis cells are small, being in division, and a lot of stomata in the phase of formation may be observed around the developed stomata.

Size of the developed (mature) epidermal elements: length of epidermal cells: 40—65 μ, their width: 24—35 μ, length of the guard cells: 37—50 μ. Joint width of guard cells: 27—31 μ. Size of the gas-exchange hose cells: 13—27 μ, their number: 1. Number of stomata: 60.

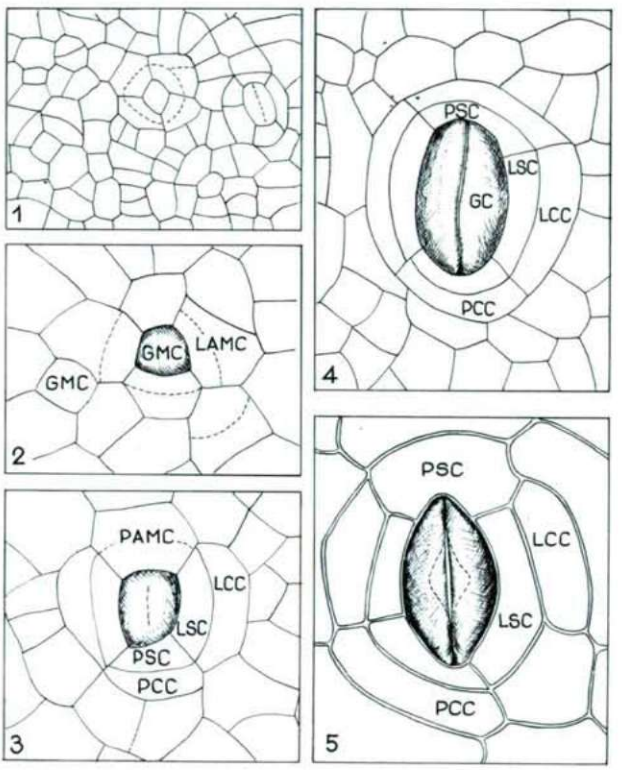

Fig. 2. Development of the stoma of *Marattia salicina*. 1—4 = dermatogenous detail in division. 5 = a fully developed stoma. G. M. C. = guard mother cell, L. A. M. C. = lateral adjacent mother cell. P. A. M. C. = polar adjacent mother cell, L. S. C. = lateral subsidiary cell, P. S. C. = polar subsidiary cell, L. C. C. = lateral coronal cell, P. C. C. = polar coronal

D) OSMUNDACEAE

6. Osmunda regalis L.

(Fig. 3, 4)

The development of the epidermis of the *Osmunda regalis* is similar to that of the *Marattia salicina*. At the rim of the leaf-primordium, in the width of 1—2 cell lines, a distal region consisting of cells of the size of 27x43 μ may be observed. Below the distal region the leaf-primordium (even that of the size of 10—15

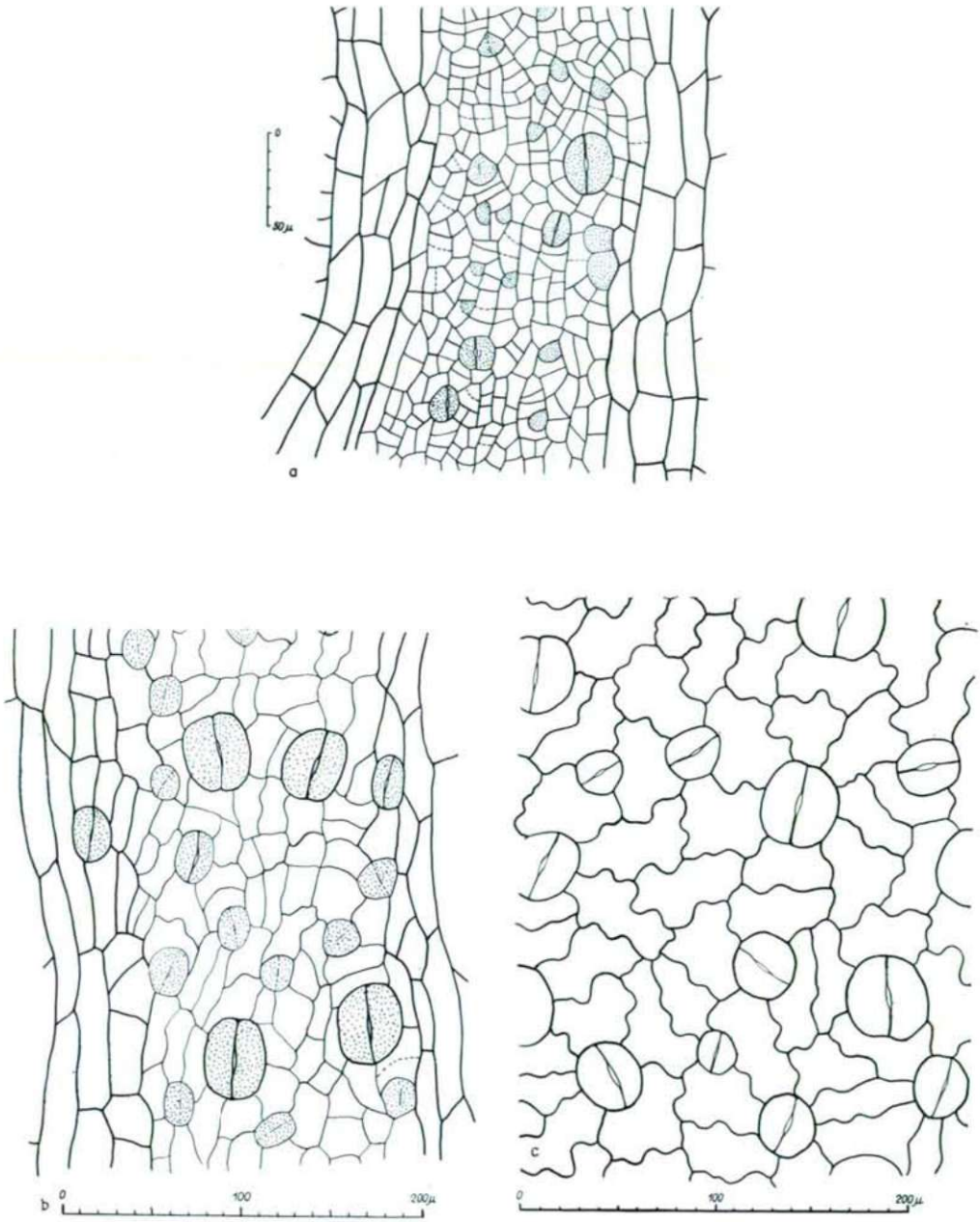

Fig. 3. Histogenesis of the epidermis of *Osmunda regalis:* a) In the intercostal field some dermatogenous cells divide in two, the distal cell becoming the guard mother cell, b) and, c) The guard mother cells enlarge and divide in two.

mm) divides on its whole surface, and protodermis cells, guard mother cells are produced in number, size and shape characterizing the species. The produced cells elongate on the whole surface, and then they get into the phase of ripening.

Formation of the stomata. The formation of the guard mother cells is similar to that of *Marattia*. From the distal end of the dermatogenous cell or from one of its corners a guard mother cell is produced by formation of concave cell walls. The basal cell of the dermatogenous cell is transformed into an epidermis cell in the way of division. The produced G. M. C. is initially surrounded by 4—5 adjacent mother cells. These cells divide at right angles to the perimeter of the guard mother cell, forming epidermis cells. Thus the developed guard cells are surrounded by 5—9 epidermis cells. If the guard mother cells are produced beside one another — what frequently occurs in the case of *Osmunda regalis* — so twin stomata are produced.

The so developed guard cells enlarge, then they divide in two by a longitudinal wall. The guard mother cell is generally smaller than the proximal epidermis mother cell. The axis of division is mildly concave. Around the guard mother cell the adjacent mother cells are in an intensive division. The adjacent mother cells frequently divide only in right angles to the developed guard. cells. There aren't produced any accessory cells. We call that form of the ontogeny of stoma haplocheil and its structure acyclical. The genesis of stoma is not purely haplocheil, it shows a transition towards the hemisyndetocheil type, as well.

Length of the guard mother cells (G. M. C.) after their genesis: 15 μ, their width: 13 μ. Length of G. M. C. before its division in two: 29 μ, its width: 23 μ. Number of stomata of a 14 mm leaf-primordium: on the summit of the leaf: 11, end the little of the leaf: 27, on the basis of the leaf: 40.

Length of the developed two guard cells: 44—63, μ, their joint width: 42—56 μ. Number of stomata: 126. Number of twin stomata: 8.

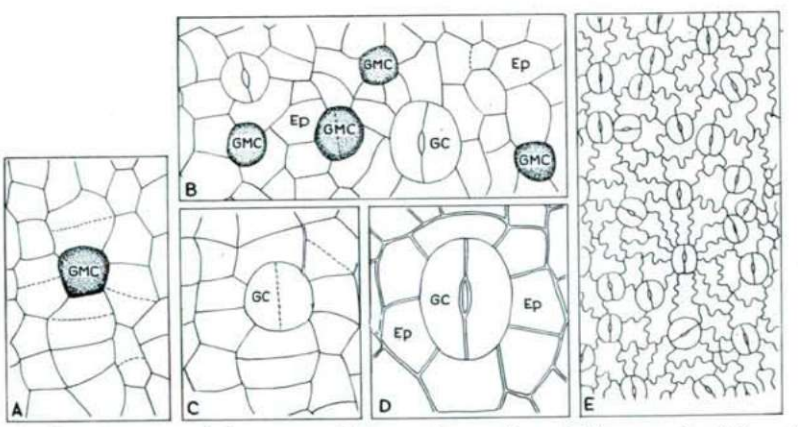

Fig. 4. Development of the stoma of *Osmunda regalis* and histogenesis of its epidermis: A = epidermis formation of the leaf-primordium of 6 mm size, B—D: that of 14 mm size, E = developed abaxial epidermis.

E) SCHIZAEACEAE

7 Schizaea dichotoma (L.) SMITH.

(Fig. 6)

In the development of the epidermis a zonal arrangement may be observed. The distal region is meristematic is nature and takes place in a cell line at the apex and two sides of the primordium. The subdistal region lies in a width of 4—5 cell lines on the apex and in 3—8 cell lines on the two sides of the leaf-primordium. This region is the centre of division. The apical part, the apical meristems ensure the longitudinal growth of leaf, producing the marginal meristems, as well as the stomatorial lath initials. The apical meristems, divide with walls forming a rigth angle to the longitudinal axis of the leaf and the marginal meristems with nearly parallel walls.

The unilinear stomatorial lath initials protruding from the surface of dermatogen, differring in shape and function and having meristematic properties are differentiated in the organization region. The guard mother cells and polar accessory mother cells develop here. The subdistal and organization regions make a transition into each other. Then, in the subspical region, the cells become much longer, getting into the phase of maturation.

Formation of the stoma: the primary mother cells of the stomatorial lath divide in two producing semicircular cell walls in the organization region. From the distal and outer tangential parts of the primary mother cell the guard mother cell and form its basal part the polar subsidiary mother cell are produced. The guard mother cells protrude from the stomatorial lath, enlarge considerably, dissolve the walls of accessory cells below themselves, and then divide in two with a longitudinal wall. The genesis of stoma is, therefore, hemisyndetocheil, its structure is diacyclical as a subsidiary cell is connected with each of the two poles of guard cells. The axis of division is thoroughly concave.

Size of the developed epidermis elements: Length of guard cells: 78—86 μ. Joint width of both guard cells: 66—74 μ. Distance between stomata: 50—124 μ. Number of stomata: 11.

8. Anemia rotundifolia SCHRAD.

(Fig. 5, 6, 7)

The formation of epidermis shows a zonal separation. The distal region takes place in a 20—35 μ wide strife on the rim of the leaf-primordium. These rim cells are 3—4 cell-lines wide, their shape in an oblong ended in a sharp point or that in a right angle to the vessels of leaves. Length of cells: 25—48 μ, their width: 8—11 μ. In the vacuolized plasma of cell there cannot be observed any chloroplastic. This region loses its meristematic property at the beginning of its formation, ensuring the defence of the subdistal region which takes place under it.

The subdistal zone is 160—200 μ wide and cannot be separated sharply from the organization region. This region is 4—6-angled, consisting of meristematic cells with big nuclei. Size of cells: 7x7,5 μ.

The organization region takes place in a 1900—2800 μ wide strife below the subdistal zone. The dermatogenous cells divide (new dermatogenous cells are produced) and are organized here. The stomata are formed here. Size of cells: 9,5x11 μ.

Below the organization region in the submarginal region the cells elongate, the chloroplastics enlarge, the nuclei are stained homogenously, the radial walls of cells have a wavy course. In the zone of maturation the cells get their definit form.

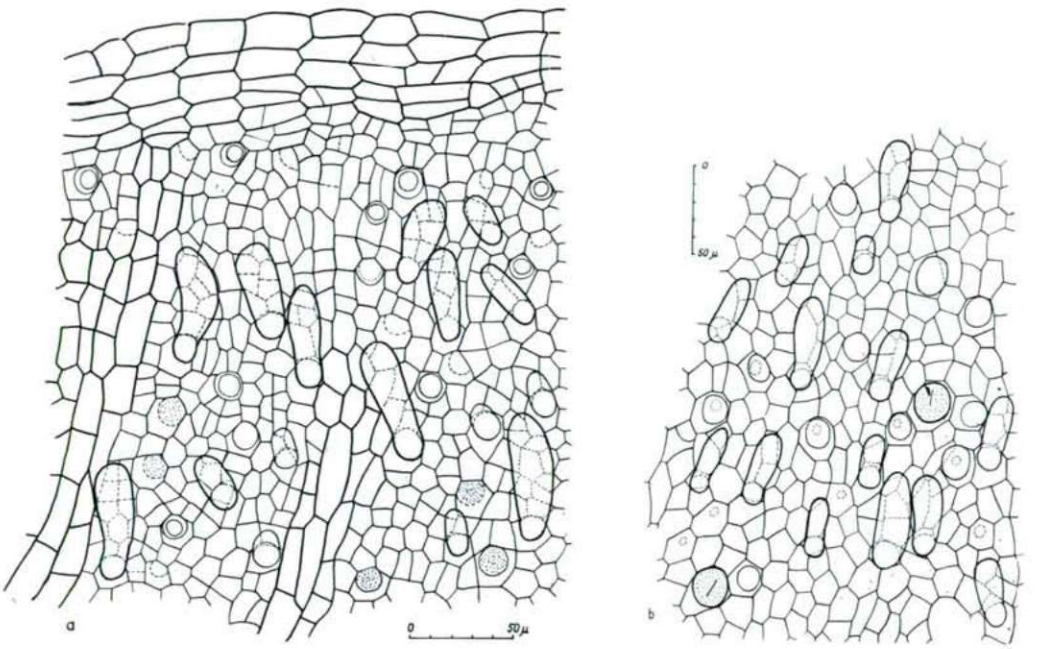

Fig. 5. Histogenesis of the epidermis of *Anemia rotundifolia:* (a) the d = distal, sd = subdistal and o = organizational regions in the lower epidermis of the leaf primordium. (b) In the organization zone the genesis of trichoma and that of the guard mother cells may be observed.

The stomata and trichomata are produced in a 1900—2000 μ wide strife. The trichomata are produced rather at the beginning of the organization region. The guard mother cell and trichoma mother cell are produced in a similar way. A spheroid knob appears centrally on the outer tangential wall of the dermatogenous cell and nearer to the distal end of the dermatogenous cell. This knob, which is at the beginning lens-like, later coniform, becomes the guard mother cell and trichoma mother cell; and the basal located cell, surrounding the G. M. C. which is at the beginning caved in and later ring-like, becomes the accessory mother cell. Later the developments of trichoma and guard cell differ from each other. The exact course of the ontogeny of the stoma can be got by the examination of

cross-sections. At some of the dermatogenous cells the outer tangential walls protuberate, the centrally located nuclei divide nearly in right angle to the surface of the leaf (in an angle of 30—45 degrees). The cell wall is formed in the shape of a hemisphere or cone towards the inside of the cell. The upper cell is the guard mother cell, the lower one is the subsidiary mother cell. The coniform G. M. C. turning with the point of cone to the mesophyllum, reaches the inner tangential wall of the subsidiary mother cell, and the cell wall dissolves at the site of touch. Therefore a round hole is produced in the subsidiary mother cell, viewed from above. Them the cells, enlarge, the guard mother cell divides in two with a longitudinal wall, the two guard cells are formed centrally, as well as a ring-formed subsidiary cell protruding from the surface and fully surrounding the former ones. We consider this genesis of stoma to be of hemisyndatocheil type and of unicyclic structure. The axis of division is thoroughly curved. It can be derived from the concave axis of division.

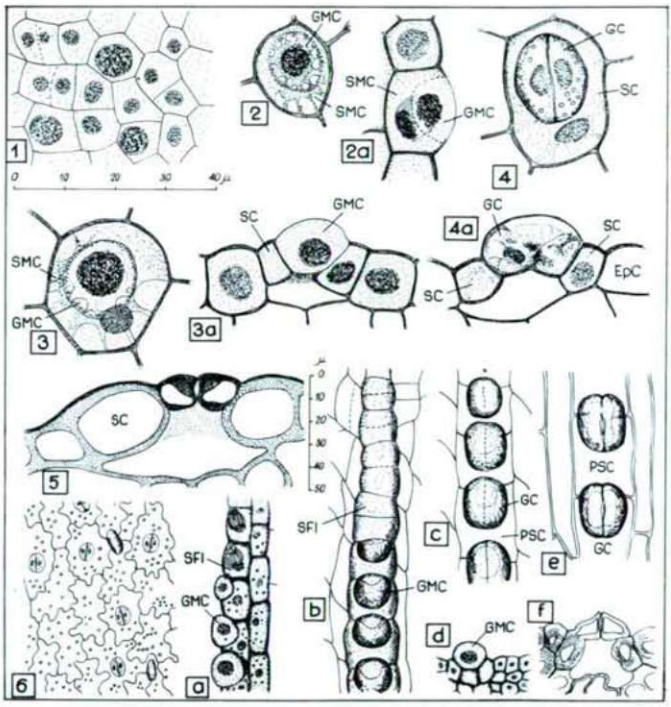

Fig. 6. The ontogeny of the stomata of *Anemia rotundifolia* (1—6) and *Schizaea dichotoma* (a—f). GMC = guard mother cell, SMC = subsidiary mother cell, SFI = stomatorial field initials, GC = guard cell, EPC = epidermal cell, ASP = air-spaces of the stoma. The degree of magnification is indicated beside the drawings. One graduation is equal to 10 μ.

The development of the trichoma differs from that of the guard cell only so far that its mother cell does not divide in two but it elongates and forms a unicellular point.

Size of the elements of the epidermis of the leafprimordium of *Anemia rotundifolia:* length of the divided GMC: 14 μ, its width: 13 μ. After division in two, the length of G is: 17 μ, the joint width of both guard cells: GC: 16 μ. Length of the mature GC: 26 μ, and its width: 22 μ. Number of guard mother cells: 20—58. Number of stomata: 18—36.

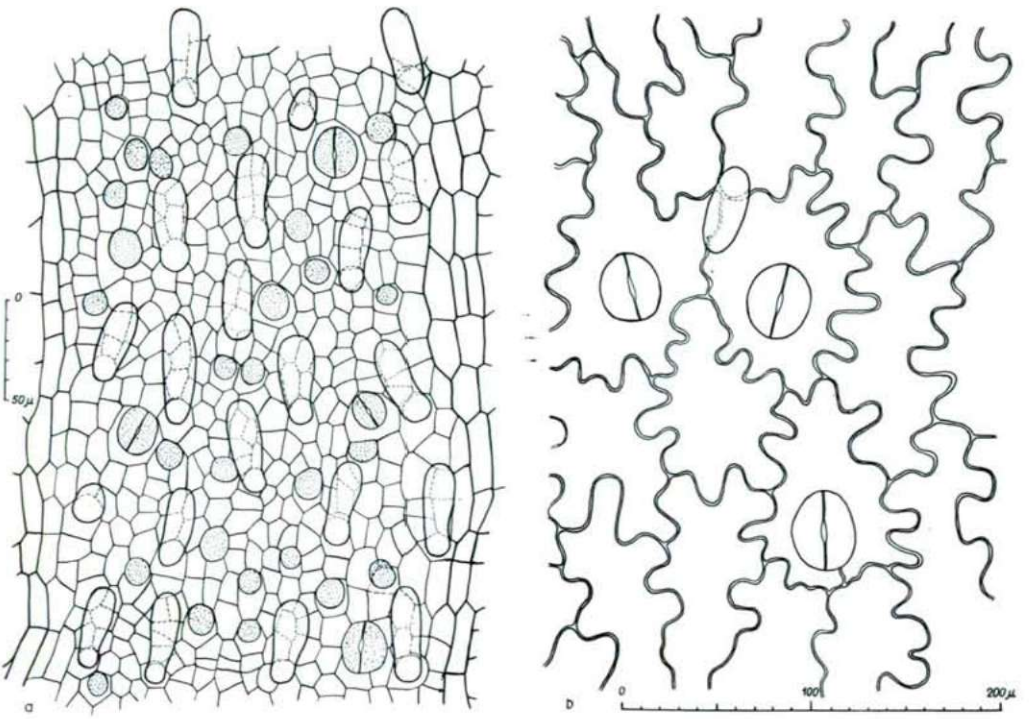

Fig. 7. Histogenesis of the epidermis of *Anemia rotundifolia:* (a) Development of the guard mother cells (dotted) in the lower epidermis. (b) The developed abaxial epidermis.

F) GLEICHENIACEAE

9. Stromatopteris moniliformis METT.

(Fig. 8)

Genesis of the leaf-slice: Two 64 μ high knobs of 8—9 cells appear in the organization region of apical meristems of the primordium of leaf-stalk, within the distance of 900—1200 μ from the apex. On the apex of the knob a big prism-shaped cell may be observed. The so produced primordium of leaf-slice elongates in the direction of apex, and later it develops in a semicircular shape by the division of the marginal meristems.

The development of the leaf-epidermis shows a zonal structure. The distal region consists of cells meristematic in nature, one cell-line wide and of 25x38 μ size. The subdistal region takes place in a semicircular strife below the rim of the leaf. In younger age, it is 200—160 μ wide, later on, after the formation of the leaf, it decreases gradually and becomes 80—55 μ wide. This region is the centre of the meristems. In the organization region (in the width of 900—200 μ) the stomata are produced in lines. The organization region decreases similarly with the growth of the leaf from the basis to the margin. In the submarginal zone the cells enlarge, the radial walls of cells become wavy. That region enlarges gradually after the formation of the leaf.

The development of stoma takes place in the organization zone. The distal end or the corner of the dermatogenous cells divides in two with a concave cell-wall formation. The distal, a little protruding cell of rounded off shape becomes the guard mother cell (GMC), the crescent shaped basal cell becomes the polar subsidiary mother cell (PSMC). The guard mother cell divides with a longitudinal cell (PSMC) derive from a common cell. The structure of stoma is diacyclic (rarely monocyclic) as two polar accessory cells join the end of guard cells. The accessory cells differ scarcely from the other epidermal cells. Size of the developed GMC: width: 20 μ, length: 16 μ. Size of the divided GMC: width: 37 μ, length: 39 μ. Size of the ripe stomata: length of the guard cells: 68—81 μ. Joint width of both guard cells: 64—71 μ. Length of the pore of stoma: 24—29 μ. Number of stomata: 73.

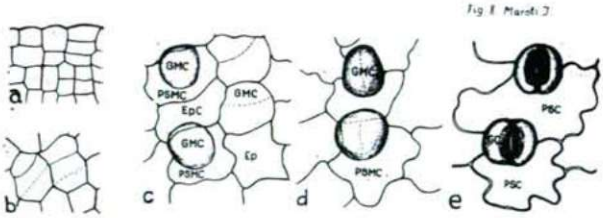

Fig. 8. Deveplomeht of the stomata of *Stromatopteris moniliformis*. KMC = guard mother cell, PSMC = polar subsidiary mother cell, EpC = epidermal cell.

G) ASPLENIACEAE

10. Asplenium viride Huds.

(Fig. 9)

The development of the epidermis of the leaf demonstrates zonal structure. The distal and subdistal regions take place at the rim of the leaf-primordium, 160—70 μ wide. The two regions cannot be separated sharply, both are meristematic in nature. These regions consist of polygonal cells of big nuclei. The subdistal region is large at the beginning, later on, however, it decreases gradually while the leaf develops.

The organization region is located below the subdistal region, parallelly to the rim of leaf, in a 700—250 μ. wide strife. Here the stomata are formed and the chloroplastics appear. The organization region is large, later on, however, it decreases while the leaf develops.

The elongation and maturation zones of the epidermis demonstrate a prog-syndetocheil because the guard mother cell and the basal polar subsidiary mother wall and transforms into a guard cell. We call this ontogeny of the stoma hemi-ressive size while the leaf develops.

The formation of stoma takes place in the organization zone. The distal end or corner of some dermatogenous cells becomes guard mother cell with the formation of concave cell walls; the basal end of the dermatogenous cell remains bigger and it becomes the polar subsidiary mother cell. The guard mother cell becomes larger and divides into two guard cells with a longitudinal wall. The crescent-shaped polar subsidiary mother cell turns immediately into an accessory cell or it divides in two forming a crescent-shaped cell wall, producing so a polar subsidiary cell and a polar coronal cell. This form of the genesis of stoma is hemisyndetocheil, its structure is monocyclic with a polar subsidiary cell.

Size of GMC in the time of formation: 7,5x8 μ. Length of the dividing GMC: 15 μ, its width: 11 μ. Length of the mature guard cell: 54 μ, and the joint width of the two guard cells: 28 μ. Number of stomata: 72.

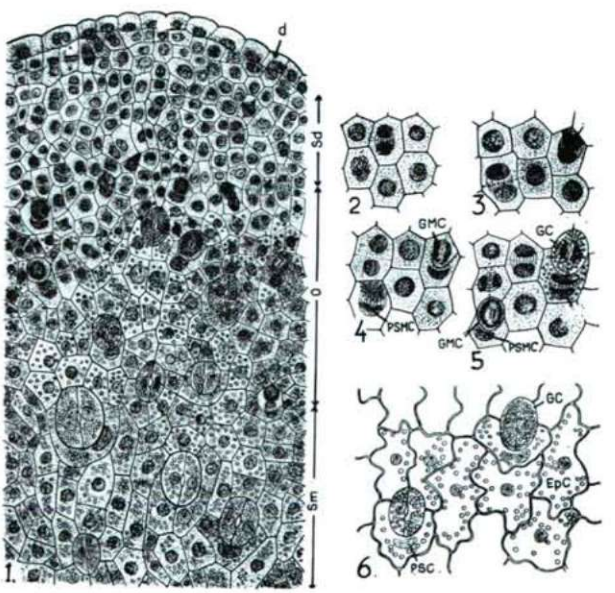

Fig. 9. Histogenesis and stoma formation of the abaxial epidermis of *Asplenium viride*. d = distal region, sd = subdistal region, o = organization region, sm = submarginal region, GMC = guard mother cell, PSMC = polar subsidiary mother cell, GC = guard cell, PSC = polar subsidiary cell, EpC = epidermal cell.

H) LOXSOMACEAE

11. Loxsoma cunninghamii R. Br.

(Fig. 10)

The formation of leaf-primordium is carried out zonally. At the rim of the leaf-primordium a less meristematic, 18—25 μ wide distal region takes place. The shape of cells is an elongated oblong in right angle to the rim of leaf. In this region the division is performed mainly with two axes of division in right angle with each other. Size of the cells: 16x22 μ.

The subdistal region is 340—60 μ wide. In the subdistal region the plane of cell division is chnging. The subdistal region is originally large, then it decreases gradually with the formation of leaf. Size of cells: 12x13 μ. This region is the centre of division.

The organization region takes place below the subdistal region in 14 000—2000 μ width. Here the mesophyllum differentiates, the stomata and chloroplastics are formed. The organizational zone cannot be separated rigidly from the subdistal zone. The plane of cell division is often concave.

The elongation or maturity zone of the leaf demonstrates a progressive size while the leaf develops.

The development of stomata takes place in the organizational zone. Some dermatogenous cells divide in two with a concave cell wall: into a lateral subsidiary mother cell ($LSMC_1$) and lateral slice mother cell (LSIMC). The latter one divides again (maybe more times) with a cell wall which is concave related to the former division wall. Thus originates the guard mother cell (GMC) of central location and the lateral subsidiary mother cell or the l. s. m. cells $LSMC_2$ or $LSMC_3$. The LSIMC is smaller than the $LSMC_1$. The $LSMC_2$ is smaller than the $LSMC_1$.

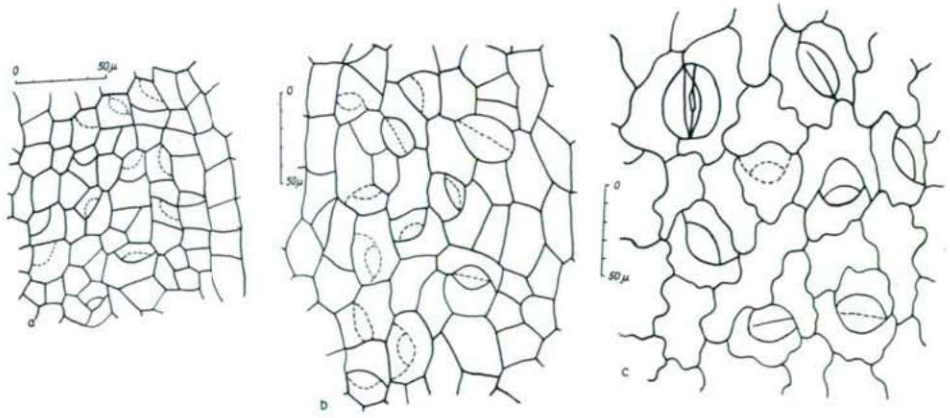

Fig. 10. Histogenesis of the abaxial epidermis of *Loxsoma cunninghamii* and the genesis of the syndetocheil stoma.

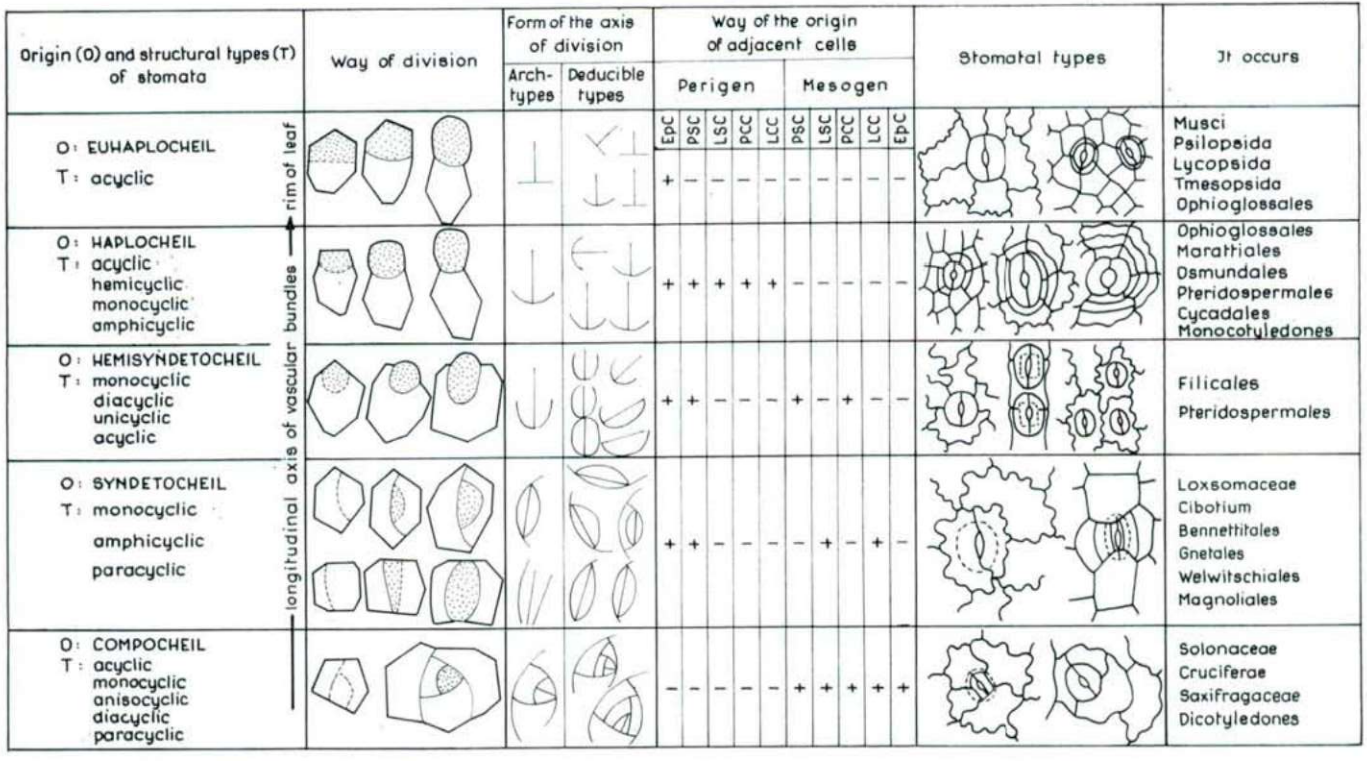

Fig. 11. Change of the area of the epidermal cells and of the number of guard mother cells (GMC) from the apex of leaf towards the basis on the leaf-primordia of *Marattia salicina*, *Osmunda regalis*, and *Anemia rotundifolia*.

The form of the axis of division is concave turned to face each other, its direction is changing, being often parallel with the longitudinal axis of the leaf vessel. From a primary mother cell dominating three, rarely four mother cells are produced.

From the lateral subsidiary mother cells lateral subsidiary cells of mesogenous origin, from the guard mother cells guard cells are produced. The guard mother cell viewed from above is similar to a biconvex lens. The Gm is gradually forced under the two lateral subsidiary cells. In the produced stoma the guard cells are thoroughly immersed.

We call this form of the stoma formation syndetocheil. The structure of stomata is paracyclic. The syndetocheil way of formation may be derived from the haplocheil one.

Size of the primary mother cell: 13x15 μ. Size of the LSMC$_1$: 8x17 μ. Size of the LSIMC: 7x14 μ. Size of the LSMC$_2$: 7x16 μ. Size of the GMC: 15x18 μ.

Discussion

A) Histogenesis of the epidermis

The development of the examined leaf of *Psilotinae* and *Filicinae* takes place in a similar way. A multicellular knot, the leaf-primordium initiative appears on the apical meristems of the shoot, and the leaf develops from that. The site of appearance, form, size, number of cells, the dominating direction of the meristematic activity of the multicellular knot are characteristic of families, species.

The development in space and time of the epidermis of the examined eleven species demonstrate a zonal structure. The regions established by WARDLAW (1957) for the structure of shoot are available also for th formtion of the leaves of *Tmesipteris* and *Filicinae*. The similar ontogenesis of both the shoots and leaves of *Psilotinae* and *Filicinae* refers to the shoot-origin of the leaves of *Psilotinae* and *Filicinae*.

Also the constitution of mesophyllum is well demonstrated by the development of epidermis. The distal regions of the leaf-primordia of the examined species are of different size, shape and meristematic activity. The distal zones of *Tmesipteris* and *Anemia rotundifolia* lose gradually their meristematic qualities after the formation of the multicellular knob.

Similarly few divisions may be observed in the distal regions of *Osmunda regalis* and *Marattia salicina*, and the division is dominating in the transversal direction. The distal regions of *Schizaea, Stromatopteris, Asplenium* have meristematic qualities. The distal region of *Tmesipteris* is large, 500—1400 μ, that of *Filicinae* is 1—4 cell-line wide.

The subdistal part is originally progressive, later on it shows a regressive size as the leaf-primordium is growing. This region is the centre of meristems. The size, form, activity, size and shape of cells of the subdistal region are characteristic of species, family. The subdistal region cannot be separated rigidly from the organization zone. In case of *Marattia* and *Osmunda*, the epidermis divides and is organized, as well, on the whole surface of leaf-primordium.

In the organizational zone the stomata, chloroplastis are produced, there begins here the elongation of cells and the nucleus gets here into equilibrium.

In the elongation and maturity zones the epidermal cells get their size and shape characteristic of the species. In the size of the dermetogenous initial cells of the subdistal region the definitive size of the epidermal cells is given. From the smaller dermatogenous cells there become smaller epidermal cells, from the bigger ones, of course, bigger cells.

B) Types of the ontogeny of stomata

Apart from the way of formation of the epidermis, the development and structure of stomata demonstrates the best how developed and differentiated the family and species are. In the course of examining the ontogeny of stomata we have taken into consideration the following factors:

(a) From how many dermatogenous cells does the stoma develop?
(b) With what kind of division is the guard mother cell formed?
(c) Plane of cell division?
(d) Where do develop the guard mother cells?
(e) From which end of the dermatogenous cell is produced the guard mother cell?
()f How do the stomata definitely develop?

On the basis of my examination we have distinguished, concerning the genesis of stomata, five main types of development:

(I) Euhaplocheil type: DC → GMC
||
EMC → EpC

(a) The dermatogenous cell divides into two cells of equal size: a guard mother cell (GMC) and epidermal mother cell (EMC) of proximal site.

(b) The plane of cell division is straight or it is nearly identic with that of the dermatogenous cells and their direction.

(c) From an epidermal mother cell only epidermal cell may develop.

(d) The cubature of the developed two guard cells is nearly the same as that of an epidermal cell.

Structure of stomata: acyclic.

Occurrence: in cases of *Psilotum, Tmesipteris, Ophioglossum, Botrychium* and *Bryophytae.*

(II) Haplocheil type: DC → GMC
EMC → EpC
perigenous PSC

(a) The dermatogenous cell divides into two cells of non-equal size: a guard mother cell and epidermal mother cell of proximal site.

(b) The plane of cell division is dominatingly in right angle to the longitudinal axis of the vascular structure of leaf, its shape being mildly concave.

(c) From an epidermal mother cell epidermal cell may develop or, with secondary division, a perigenous polar subsidiary cell (PSC).

(d) The cubature of the developed two guard cells is greater than that of an epidermal cell.

(e) Around the developed guard mother cell the perigenous division of the adjacent cell is frequent.

Structure of stomata: acyclic, hemicyclic, monocyclic, amphicyclic.

Occurrence: *Ophiolossum, Botrychium, Helminthostachys, Osmunda, Marattia, Angiopteris, Cycadales.*

(III) Hemisyndetocheil type- DC → GMC
PSMC → mesogenous PSC

(a) The dermatogenous cell divides into a smaller guard mother cell (GMC) and a bigger polar subsidiary mother cell of proximal site (PSMC).

(b) The plane of cell division is in right angle to the longitudinal axis of the vascular structure of leaf, its shape is thoroughly concave.

(c) The PSMC differs in shape, size, shape of nucleus from the other dermatogenous cells.

(d) From the PSMC a polar subsidiary cell PSC may be produced immediately (without division), in mesogenous way, or polar subsidiary cell (PSC) and polar coronal cell (PCC) in an indirect way (with division).

(e) The cubature of the developed two guard cells is generally smaller than that of an epidermal cell.

Structure of stomata: monocyclic, unicyclic, diacyclic, acyclic.

Occurrence: As a rule, at species of *Filicinae Leptosporangiatae.*

(IV) Syndetocheil type: DC → LSIMC → GMC
LSIMC → $LSMC_1$
LSIMC → $LSMC_2$ – mesogenous LSC

(a) The dermatogenous cell divides in two cells: into a lateral subsidiary mother cell ($LSMC_1$) and a lateral slice mother cell (LSIMC). The lateral slice mother cell is again dividing with a cell wall which is concave towards the former division wall, and a guard mother cell (GMC) is produced in central position plus a lateral subsidiary mother cell ($LSMC_2$).

(b) The plane of cell division is dominating parallel with the longitudinal axis of the vascular structure of leaf, its shape is concave as opposed.

(c) The $LSMC_1$ is larger than the $LSMC_2$.

(d) From the lateral subsidiary mother cell a lateral subsidiary cell (LSC) may be produced in an immediate way (without division) or a lateral subsidiary cell and a lateral coronal cell (LCC) may be produced in an indirect way (by division). There are frequently stomata at which there are on the one side LSC and

LCC, on the other one, however, only LSC. In this case the GMC is produced after the third division.

(e) The polar subsidiary cells of mesogenous origin are missing. PSC of perigenous origin may, however, be produced.

Structure of stomata: paracyclic, monocyclic.

Occurrenced: Loxsoma, Cibotium species.

$$\text{(V) Compocheiltype: DC} \rightarrow \text{LSIMC} \xrightarrow{\text{n divisions}} \begin{matrix} \nearrow \text{AMC}_1 \\ \text{GMC} \\ \searrow \text{AMCn} \end{matrix}$$

(a) The dermatogenous cell divides into two cells: into adjacent mother cell one (AMC_1) and a slice mother cell (LSIMC). The slice mother cell separates after n divisions into a guard mother cell (GMC) and n adjacent mother cells (AMCn).

(b) The plane of cell division is changing, it is generally in right angle to the axis of division, its shape is mildly concave, being turned back.

(c) From the adjacent mother cell there may be produced an epidermal cell, subsidiary cell, and coronal cell in a direct or indirect way.

(d) The adjacent cells are of mesogenous origin.

Structure of stomata: acyclic, anisocyclic, monocyclic, diacyclic.

Occurrence: *Solanaceae, Cruciferae, Saxifragaceae.*

From the *Angiosperms* we have observed the ontogeny of the stoma of these few families. We suppose that the majority of the dicotyledonous plants belong into this type from the point of view of the ontogeny of stomata.

Fig. 11. Types of the history of development of the genesis of stomata.

Summary

(1) The leaf formation of the examined eleven species demonstrates a zonal structure in space and time. The regions ascertained by WARDLAW (1957) for the organization of shoot are valid to the formation of *Tmesopsida* and *Pteropsida* leaves, as well. In the course of the organization of the leaf primordium, distal, subdistal, organizational, lengthening, and ripening zones were distinguished.

(2) The histogenesis and structure of leaf mirrors he degree of he development of species, as well its natural taxonomical place.

(3) The skin tissue is the most suitable of the tissues of leaves for comparative histogenetic examinations, especially concerning the development and structure of stomata.

(4) In the course of our examinations, five archetypes of the history of development of the genesis of stomata have been distinguished: euhaplocheil, haplocheil, hemisyndetocheil, syndetocheil, and compocheil ones.

References

BOWER, F. O. (1935): Primitive Land Plants, also known as the *Archegoniatae*. — London.

BRITTON, E. G. and TAYLOR, A. (1909): Life history of *Schizaea pusilla*. — Bull. Torr. Bot. Cl. — Lancaster, *28*, 1—19.

FLORIN, R. (1931): Untersuchungen zur Stammesgeschichte der *Coniferales* und *Cordaitales*. — Almquist et Wiksels, Stockholm.

FLORIN, R. (1933): Über die *Cycadales* des Mesozoikums nebst Erörterungen über die Spaltöffnungsapparate der *Bennettitales*. — Stockholm.

HILDEBRAND, F. (1866): Über die Entwicklung der Farnkrautspaltöffnungen. — Bot. Ztg. Leipzig. *24*, 245—251.

MARÓTI, I. (1961): Untersuchung der Entwicklung der Epidermis des *Psilotinae* und des *Filicinae*-Blattes und der Entwicklung des Stomes. —Acta Biol. Szeged, *7*, 43—67.

OUDEMANS, M. (1866): Sur l'origine des stomates, de quelques espèces d' *Aneima*. — Bull. Congr. internat. de Bot. Hort. Amsterdam.

PRANTL, K. (1872): Ergebnisse der neueren Untersuchungen über Spaltöffnungen. — Flora, Seite 30.

PRANTL, K. (1881): Untersuchungen zur Morphologie der Gefässkryptogamen. Die *Schizaeaceen*. — Wilhelm Engelmann, Leipzig.

RAUTER, S. (1870): Entwicklung der Spaltöffnungen von *Aneimia* und *Niphobolus*. — Mitt. Naturw. Verein f. Steiermark. *2*, 1—38.

STRASBURGER, E. (1867): Ein Beitrag zur Entwicklungsgeschichte der Spaltöffnungen. — Jahrb. wiss. Bot., *5*, 297—342.

WARDLAW, C. W.: (1957): On the organization and reactivity of the shoot apex in vascular plants. — American J. Bot. *44*, 176—185.

ZIEGENSPECK, H. (1944): Vergleichende Untersuchung der Entwicklung der Spaltöffnungen von *Monokotyledonen* und *Dicotyledonen* in Lichte der Polariskopie und Dichroskopie. — Protoplasma, *38*, 197—224.

ZIMMERMANN, W. (1927): Die Spaltöffnungen der *Psilophyta* und *Psilotales*. — Zeitschr. f. Bot. *19*, 129—170.